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STUDIES ON THE CARYOPHYLLAEIDAE OF NORTH AMERICA

WITH SEVEN PLATES

BY

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under the direction of Henry B. Ward
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THESIS

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INTRODUCTION

There have been only a few comprehensive monographs written on the parasites of North American fish. Cooper (1918) adequately dealt with the Pseudophyllidea, omitting, however, the family Caryophyllaeidae. This group of Cestodaria has been given considerable attention during the past few years by several European writers, as Nybelin (1922), Woodland (1923, 1924, 1926), Furhmann and Baer (1925), and others. On the other hand only four papers have appeared prior to 1925 on the Caryophyllaeidae of North America. Three of these added new species to existing genera and one created a new genus to hold the form described. The writer, therefore, undertook a study of the species found on this continent together with a description of several new species and a consideration of the family Caryophyllaeidae.

The European members of this group have received much attention recently and the abundance of figures and the descriptions of the parasites particularly in the monograph on the Pseudophyllidea by Nybelin (1922), and also Woodland's (1923, 1926) papers bridged the gap where specimens were insecurable. Through the kindness of Professor Henry B. Ward the author had access to either slides or vials of original material of all four species described from North America. Dr. Edwin Linton furnished two slides of "*Monobothrium*" *terebrans* and the United States National Museum sent a vial of Linton's "*Monobothrium*" *hexacotyle*. The Museum of Zoology of the University of Michigan sent the type specimen of "*Caryophyllaeus*" *laruei* which was described by Miss Lamont in 1921. Later more of this material was found in vials of Cestodaria which had been sent by Dr. G. R. LaRue to Professor Ward. All of the original material, both slides and vials, for the descriptions of Cooper's (1920) *Glaridacris castostomi* had been added to the collection of Professor Ward and were given to me for further study.

During the past few years over 600 fish from various rivers of the central states known to harbor Cestodaria were examined by the author. A general account and summary of much of the material will be found in a paper by Essex and Hunter (1926). The summer of 1925 was spent in making examinations of living material in the field. The following summer was passed in study at the United States Fisheries Biological Station at Fairport, Iowa, on the Mississippi River. Here over 180 more fish were examined and the living parasites studied. A special trip was taken to Heart Lake, Yellowstone National Park and two trips to Lake Mendota, Madison,

Wisconsin, as well as several trips to the Rock and Illinois rivers in search of additional material. Through the cooperation of other scientists the author has had access to Cestodarian material collected from Minnesota and North Carolina.

In the main the classification followed has been that of Lühe (1910) which has subsequently been modified to include some of the forms encountered which clearly belong here.

The writer wishes to tender his thanks first to the University of Illinois which furnished material and equipment for a summer in the open and to Dr. G. W. Hunter for furnishing further assistance; to the entire staff of the United States Bureau of Fisheries Biological Station at Fairport, Iowa, through whose cooperation it was possible to carry on research work; to the Illinois State Natural History Survey for the loan of equipment and to Dr. D. H. Thompson who supplied many of the fish; to the Zoological Laboratory of the University of Wisconsin for the privileges extended while there; to the United States National Museum for vials of material; to the Museum of Zoology, the University of Michigan for the type specimen of "*C.*" *laruei;* to the Biological Laboratories of the Rensselaer Polytechnic Institute; and to the following investigators for help: Dr. Edwin Linton, University of Pennsylvania; Dr. H. J. Van Cleave, University of Illinois; Dr. George R. LaRue, University of Michigan; Dr. David H. Thompson, Illinois State Natural History Survey; Dr. Parke H. Simer, Illinois Wesleyan University; Dr. Hiram E. Essex, Mayo Clinic; Dr. Fred J. Holl, University of Buffalo; Wanda Sanborn Hunter, and to others, who, as fellow students have cooperated in many ways, gratitude is expressed.

Particularly to Professor Henry B. Ward the writer wishes to express his sincere appreciation, not only for procuring type specimens, vials of material, loaning much material from his own collection and extending the privileges of his extensive library, but also for the guidance and helpful criticism which has given me the inspiration to complete this work.

METHODS AND SOURCES OF MATERIALS

The methods used in making this study vary somewhat from those usually employed. First a summary of the sources of material will be given, followed by a description of the methods employed in securing the parasites and finally the methods of preservation and study.

The material in the field was supplied to a large degree by the commercial fishermen. A superficial examination and identification of the host was first made. Later the heads and viscera were supplied for further examination. Such methods permitted a thorough examination of the host, and fish which were unusual in any respect were then secured from the fishermen. This method was employed during the summer of 1925 in the field by Dr. H. E. Essex and myself. The next summer was passed by the writer at the U. S. Fisheries Biological Station at Fairport, Iowa. Here fish were supplied by the crew of the Station who seined them from the Mississippi River, placed them in tubs, and brought them back alive where they were placed in cement lined ponds until examination was possible. As the writer always accompanied the crew on the trips fish were examined as soon as they showed signs of dying.

A third source of material should be noted. The writer made several trips to neighboring streams and by offering to clean the fish that were caught he was able to secure host records and make examinations of numerous viscera for parasites. Through the kindness of Dr. David H. Thompson of the Illinios State Natural History Survey and the cooperation of Mr. "Mike" Hunt fish were shipped on ice to me during the fall and early spring, thus examinations were made which covered nearly the entire year. Through the cooperation of Dr. Parke H. Simer records were secured of hosts taken near Money, Mississippi. Additional material was obtained from Burntside Lake, Minnesota, Lake Erie, New York, and the Eno River, North Carolina.

When in the field the viscera were opened up and macroscopic and microscopic examinations were first made. Then the stomach and intestines were opened, the parasites and the food removed and placed in a normal salt solution pending further study. The intestines were then scraped with a scalpel, the scrapings reëxamined under a lens, and the remainder of the visceral mass was examined under a hand lens magnifying 8 diameters. During the summer of 1925 a compound microscope and a portable Spencer dissecting microscope with a maximum magnification of 20 diameters were used. This facilitated the detection of plerocercoid larvae less than 0.5 mm. in length.

Another method employed while in the field should be outlined at this point. The stomachs and intestines were opened, the contents placed in various bottles containing normal salt solutions and labelled "stomach," "upper third," etc. When these were shaken, and the debris decanted off the parasites remained in the bottom of the bottles. A microscopic examination of the stomach and intestines always followed this method. This procedure secured all of the parasites except those 1 mm. or less in size, and is good to use in the field when speed is necessary.

Later a third method was tried. The contents of the stomach and intestine were emptied into a cone shaped plankton net made of bolting-cloth. Another piece of this cloth was placed over the mouth of the faucet to strain out the crustacea, etc. The water was then run through the plankton net; this washed out all of the material except the parasites which were thus concentrated in the bottom of the net. This method may be modified so that the stomach contents are washed first, thus keeping accurate records of the location of the parasites.

After the living parasites were secured they were always placed under the microscope and their methods of movement, type of scolex, length, breadth, translucency, etc. were noted. A study of this nature served to convince me that the scolex possesses certain fundamental characters which are of value in classification. For although the parasites may elongate the scolices nearly 100 percent, the same general shape is usually retained throughout, and if loculi are present they may be seen at all times. On the other hand, there are scolices which are so well formed as to be practically immobile, i. e. *Capingens singularis*. This observation is rather significant when it is found to be generally true in the case of a hundred specimens or more, as was the case with *Hypocaryophyllaeus paratarius*. When it was desirable to keep the parasites alive for some time it was found that they would live up to 72 hours in Ringer's Solution without the dextrose.

FIXATION AND PRESERVATION

In the beginning a number of fixatives were tried, but it was soon determined that the best results were obtained after using either Bouins' (picro-formol-acetic), or a saturated aqueous solution of mercuric chloride. These fluids were allowed to act for about 1 to 2 hours and the materials were passed through 50% alcohol and 70% iodized alcohol. Great care must be taken to remove all of the mercuric chloride as otherwise the material will be ruined.

The stain used for toto mounts and sections was Ehrlich's acid hematoxylin and Delafields' hematoxylin mixed half and half. Stains with either one of the reagents mentioned above or with Conklin's modified hematoxylin also gave good results. To secure the best results, however, it was necessary to stain in a full strength solution for several days, destain in

10% acid alcohol (made acid with hydrochloric acid). After destaining the parasites should be transferred to a saturated sodium carbonate solution in 85% alcohol to which had been added 3 to 4 drops of ammonia per 100 cc. In this manner the internal organs could be stained heavily and the outer portions destained rapidly with acid alcohol. The material could then be run up into the clearing agents where it was possible to make drawings before sectioning. Various clearing agents were used, such as benzol, xylol, methyl salicylate (synthetic oil of wintergreen), and cedar wood oil. The last two did not harden the material as much and in the case of embedding it was not necessary to remove all of the cedar wood oil from the paraffin, as was the case with the xylol group. The sections were counterstained with eosin and orange G. One slight change in the usual method of embedding was adopted. The parasite was infiltrated with parawax (melting point about 44 degrees centigrade). This object was then transferred directly to the embedding boat which had just been filled with paraffin of the desired melting point. This gave a block which had an outer hard layer of paraffin while the object itself was filled with parawax, thereby insuring smooth cutting with a minimum of vibration. By following this method excellent sections were secured.

Inasmuch as the testes number is very constant in the adult parasites of this group and varies in the different species from about 50 to over 400, a method for the accurate determination of the number found in any species should be of value. Two methods were employed, depending upon whether the testes were large or small. Both were checked by an actual count of the same and other specimens, so the writer feels warranted in recommending these methods. To secure the best results material which had been cross-sectioned should be used. Furthermore, the number of sections on each row of the slide should be constant.

This first method should be used only when the testes are large so that there are not more than six or eight appearing on a section. Count, by tracing each testis, the actual number of testes in each of ten or fifteen rows. These should be picked at random, care being taken, however, to exclude the first and last rows of sections containing testes. In order to be consistent the testes which were disappearing at the left end of the row were not counted, and any part of a testis showing at the right hand edge was considered as a whole one. The average number of testes of the ten or fifteen rows was taken as the average number per row. The number of rows containing testes was then counted, and this was multiplied by the number found per row. To this was added the actual number found in the first and last rows which contained testes. This method gave very accurate results. It may be checked by the use of sagittal sections, but these are, however, more difficult and less satisfactory.

The second method should be used on forms with small testes where more

than six or eight appear on a section and has been successfully used in estimating the number of testes in cestodes as well as Cestodaria. Count the number of portions of testes visible on each section, add, and divide by the actual number of sections found to contain a single testis. This number should be determined by actually tracing through 30 to 50 testes and taking the average. This method is very accurate for parasites with small sized testes.

EXPLANATION OF TERMS

Owing to the fact that there is considerable confusion in the earliest literature regarding the orientation of the body of cestodes and Cestodaria, the writer wishes to explain the terms that will be used in the descriptions which follow.

The terms "lateral" and "marginal" are used synonymously here and correspond to the "marginal" portions of the tape worm strobila, or proglottid. Inasmuch as most Cestodaria are flattened dorso-ventrally this is fairly easy to comprehend. The "ventral" surface is the one upon which the male and female reproductive systems empty, and the "dorsal" surface is, of course, the one opposite. The end of the worm which is devoid of elements of the reproductive system or which bears the scolex, is considered as anterior, and the opposite one posterior. To insure brevity the terms "length," "breadth" or "width," and "depth" are used instead of the longer terms, "diameters in the longitudinal, in the transverse, and in the dorso-ventral directions," respectively. The term "adult" as used herein connotes parasites which show eggs in the uterus. In all the Caryophyllaeidae examined the spermatozoa are formed before the eggs so the pressence of the latter presupposes the existence of the former.

HISTORICAL DATA

The family Caryophyllaeidae was erected by Leuckart (1878) and was first adequately described in 1885 by Claus where it was placed in the tribe Caryophylloidea, along with Archigetidae. The Amphilinidae and Gyrocotylidae were placed in another tribe, the Trematodimorpha. Hoyle (1888), in writing for the *Encyclopedia Britannica*, places the Amphilinidae, Gyrocotylidae, and Caryophyllaeidae (including Archigetidae as a genus in the latter family) under the order, Monozoa, in contrast to the Merozoa, or polyzootic cestodes. This classification is essentially retained by Benham (1901) in *A Treatise of Zoology* where the class Cestoidea is divided into two grades, "A," the Monozoa and "B," the Merozoa. Then the families Amphilinidae, Gyrocotylidae and Caryophyllaeidae are raised to the rank of orders, becoming respectively Amphilinacea, Gyrocotylacea, and Caryophyllacea. Perrier (1897) places Gyrocotyle, Amphilina, Wageneria, Caryophyllaeus, Monobothrium and Diporus in the family Caryophyllaeidae. Lühe (1910) in *Die Süsswasserfauna Deutschlands* separates the Caryophyllaeidae from the Gyrocotylidae and Amphilinidae and places them as a family under the Pseudophyllidea which he describes as follows:

> Monozootische Pseudophyllideen mit unbewaffnetem und schwach ausgeprägte Sauborgane tragendem Scolex, der von dem folgenden Körper durch eine halsartige Einschnürung abgesetzt sein oder ohne solche direkt in denselben übergehen kann. Ein an seinem Hinterende die Oncosphärenhäkchen tragender Schwanzanhang kann auch beim geschlechtsreifen Tier noch erhalten sein. Genitalorgane nur in der Einzahl vorhanden. Sämtliche Geschlechtsöffnungen flächenständig, ventral, median, dem Hinterende genähert. Cirrus unbestachelt, vor den weiblichen Geschlechtsöffnungen; Vagina und Uterus münden am Grunde eines gemeinsamen Vorraumes, welcher in seinem histologischen Bau dem Genitalatrium ähnelt und sich unmittelbar hinter dem Cirrus in ein nur schwach ausgebildetes Genitalatrium öffnet. Keimstock zweiflügelig, direkt hinter den Genitalöffnungen. Dotterstöcke vor dem Keimstock, in der Markschicht, aber peripher von den Hoden und diese mantelartig umhüllend; eine Gruppe von Dotterstocksfollikeln auch im Hinterende des Körpers, von der Hauptmasse der Dotterstöcke durch den Keimstock und die weiblichen Genitalgänge getrennt. Hoden zahlreich, ausschliesslich vor dem Keimstock und den weiblichen Genitalgängen. Uterus ein geschlängelter Kanal, ohne sackartige Auftreibungen. Eier gedeckelt.
>
> Zwei Gattungen, deren Arten wenigstens im Larvenzustand in der Leibeshöhle von *Oligochaeten* schmarotzen und z. T. dort auch die Geschlechtsreife erreichen.

Cooper in writing concerning the family Caryophyllaeidae in 1920 follows Lühe whose definition he modifies to include his new species, *Glaridacris castostomi*. This was primarily a modification of the scolex characters and reads:

> Monozootic pseudophyllidea with scolex unarmed; may or may not bear more or less well expressed sucking organs which are set off from the rest of the body by a neck-like constriction or are fused with the same without such.

Nybelin (1922) makes the family, Caryophyllaeidae, of Leuckart (1878) the subfamily, Caryophyllaeinae, which he places as one of two in the new family Cyathocephalidae. This latter family is characterized as follows:

Pseudophyllideen mit anapolytischer und acraspeder Strobila. Geschlechtsöffnungen flächenständig, median, die desselben Genitalkomplexes stets auf derselben Fläche der Strobila; Mündung des Uterus zwischen denen des Cirrus und der Vagina, in innigster Beziehung zur letzteren. Germarium median gelegen, ausgesprochen zweiflügelig mit lobierten Flügeln; das Gewebe der Seitenflügel viel kompakter als das der Querbrücke. Ootyp von gut ausgebildeten "Schalendrüsen" umgeben. Uterus gewunden, ohne lokale Erweiterung und mit echter öffnung. Uterinaldrüsen gut ausgebildet. Eier dickschalig, gedeckelt.—Geschlechtsreif in Fischen (Ausnahme Archigetes).

The subfamily Caryophyllaeinae is characterized by Nybelin (1922) in these words:

Cyathocephaliden mit schwach ausgebildeten oder fehlenden Saugorganen am Vorderende, das folglich als Scolex meistens nicht abgesetzt erscheint. Germarium und Geschlechtsausführungswege nur in der Einzahl vorhanden, im hinteren Körperteil gelegen. Hodenbläschen ausschliesslich vor denselben, die ganze Markschicht erfüllend. Vas deferens vor dem Cirrusbeutel gelegen, Prostatadrüsen fehlen. Cirrusbeutelparenchym verhältnismässig bis sehr stark von Muskeln durchsetzt; Cirrus ohne distinkte Wandung. Männliche Genitalöffnung sich der weiblichen anschliessend. Münding des Atrium utero-vaginale bzw. Ductus utero-vaginalis ohne Sphincter. Vagina in ihrem ganzen Verlauf hauptsächlich nach hinten ziehend. Ausdehnung der inneren weiblichen Genitalleitungswege in der Sagittalebene, hauptsächlich von vorne nach hinten, die Lage derselben annähernd median. Der Germiduct entspringt vom hinteren Rand der Querbrücke des Germariums mit schwach ausgebildetem Schluckapparat, verläuft zuerst nach hinten, biegt dann knieförmig nach rechts oder links um und vereinigt sich mit dem schräg ventralwärts nach hinten verlaufenden Ductus seminalis zu dem sehr kurzen, mehr oder weniger dorsalwärts nach hinten ziehenden Befruchtungsgang. Der unpaare Dottergang verläuft, dorsal von der Querbrücke des Germariums, an der dem Ductus seminalis entgegengesetzten Seite des Germiducts etwas ventralwärts nach hinten und mündet nach einer halbkreisförmigen Biegung ventral in den Befruchtungsgang ein. Dotterstocksfollikel die Hodenbläschen mantelförmig umgebend, eine kleine Anhäufung von Follikeln auch am Hinterende hinter dem Germarium und den Uterusschlingen. Uterus zum grösseren Teil von Uterinaldrüsen umlagert. Eier verhältnismässig gross.

In 1923 Woodland alters his definition of the Caryophyllaeidae to include the species described by Cooper (1920), but places the genus as a synonym of Caryophyllaeus. His redefinition of the family is:

Cestodaria, usually with a slightly flattened cylindrical elongated body but sometimes fluke-shaped, devoid of calcareous corpuscles and cuticular spinelets or hooks, with an anterior end extremely variable in form and size, both in the individual and in different species, which never carries circular suckers but may bear shallow elongated grooves (different in number, form and arrangement to those found in the scolex of other Cestoda), with the cirrus and vagino-uterine apertures contiguous or nearly contiguous on the ventral surface of the body in the median line and occasionally opening into a common shallow atrium, with the testes situated anteriorly and entirely in front of the uterus, with the vagina and uterus forming a complete circuit with a common vagino-uterine opening to the exterior, with a network of excretory channels, the larger ones of which form irregular longitudinal canals about 8 or 10 in number and all of which open externally by a median posterior excretory bladder, and with

a larval form known in some cases to be hexacanth. Parasitic in the intestine of Teleostome fishes (Malacopterygii and Ostariophysi) and in the body cavity of aquatic Oligochaeta (Tubificidae).

This family he places with the Gyrocotylidae in a new order, the Paralinidea, and the Amphilinidae in another new one, the Amphilinidea. Fuhrmann and Baer (1925) point out that the Caryophyllaeidae of Woodland is equal to the subfamily Caryophyllaeninae of Nybelin (1922). They further disagree with Woodland's classification claiming that it is a regression. Woodland, however, in 1926 offers a rebuttal and endeavors to maintain his original classification. Meggitt (1924) in his *Cestodes of Mammals* accepts Nybelin's (1922) classification without change.

DISCUSSION

There is little doubt but that there are two sides to the question of the position of the Caryophyllaeidae. It is impossible, however, to settle this question until such time as the life histories of these parasites as well as those of other related groups are better known. Mrâzek, for example, in 1908 claimed to have found the larval form of *Caryophyllaeus laticeps* (=*C. mutabilis*) in tubificids. He based this only on the morphological similarities between this form and the adult. Furthermore, he laid considerable stress upon the presence of "faserzellenstränge" which at that time had only been reported for *C. laticeps*. Since then, however, there have been at least three species found which are described as possessing this character. This merely goes to show the indefiniteness incurred when one relies entirely upon morphology. In other words it does not seem logical to point to this with finality until the life histories are completely known. Until that time the decision as to the real position of the Caryophyllaeidae must wait. This will come when the life history of some of the members of the family have been proved and checked beyond doubt. Thus, after more of the life histories of the Pseudophyllidea and several of those of the Caryophyllaeidae have been solved, it will be possible to point more definitely to the true relationship, if any, which may be between them. In closing, however, let me add that the genus Capingens certainly shows some Pseudophyllidean characters. The writer, therefore, proposes for the present to follow Lühe, and leave the Caryophyllaeidae as an independent family under the Pseudophyllidea (Hunter, 1927,1929) rather than accepting Nybelin's (1922) designation as one of the subfamilies of the Cyathocephalidae.

THE GENERA OF CARYOPHYLLAEIDAE

The genus Caryophyllaeus was described by Gmelin (1790) and *C. piscium* was subsequently regarded as the monotype. This was based on Goeze's (1782) description supplemented by that of Bloch of the same date. Diesing (1850) gives this as a synonym of *C. mutabilis* while von Nordmann

as early as 1840 gives *C. cyprinorum*, *C. mutabilis*, *Fasciola fimbriata* and *Taenia laticeps* as synonyms of *C. piscium*. Rudlophi (1802:98) renames the "*C. piscium*" of Gmelin and Goeze, *C. mutabilis*. Many of the later writers followed this author, for Baird (1853), Blanchard (1888), and Diesing (1850) all used the term *C. mutabilis*. The latter author gives a long list of synonyms in which *T. laticeps* Pallas (1781) is mentioned. Others including St. Remy (1890), Looss (1892), Will (1893), Perrier (1897) and Mrázek (1901) all continue the use of *C. mutabilis*. Will in his paper makes a detailed study of this species and contributes much on the histology and cytology of *C. mutabilis*. Von Nordmann (1840) calls attention to the synonymy of *C. mutabilis* with *C. piscium*, but receives little or no notice. Lühe (1910) gives *C. mutabilis* Rud. (1802) as a synonym of *C. laticeps* (Pallas 1781). Since Rudolphi's account goes back to the "*C*(1) *piscium*" which was first described by Goeze (1782) and Pallas' *T. laticeps* antedates this year, it seems that Lühe has acted correctly. Zeder (1803) added further confusion to the synonymy of *C. laticeps* by describing this same form as *C. cyprinorum* and giving as synonyms *T. laticeps* Pallas and *Fasciola fimbriata* Goeze in Cyprinus sp. of Europe. He includes in addition the generic synonyms Caryophyllus, Caryophilinus and Phylline. Two forms were described by Schrank (1788), *Caryophyllinus communis*, and *Caryophyllinus stentoreus*. The first is based on Goeze (1782) and the second on Hermann (1783), but these were relegated to synonymy of *C. mutabilis* by Diesing (1850). More recent workers as Lühe (1910), Nybelin (1922), and Woodland (1923, 1926) have adopted *C. laticeps* (Pallas 1781) and have considered *C. mutabilis* Rudolphi 1802 as a synonym.

According to Baird (1853) there were two forms described by von Siebold, in the collection of the British Museum *C. trunctatus* in *Cyprinus nasus* and *C. tuba* in *Salmo fario*. The latter was redescribed as *Ligula tuba*, by Wagener in 1854. Molin (1858) describes "*Caryophyllaeus*" *punctulatus* and "*C.*" *trisignatus* but the figures and descriptions are so indefinite that they are of little value and cannot definitely be placed in this group. Monticelli (1892) suggests that "*C.*" *trisignatus* possesses a tetrabothriid scolex; this was also noted by Woodland (1923). Diesing (1863) created a new genus Monobothrium to hold *M. tuba*, the *Ligula tuba* of Wagener, and *M. punctulatum*, the "*C.*" *punctulatus* of Molin. Monticelli (1892) places *M. tuba* (from *Tinca chrysitis*) and *M. punctulatum* (from *Conger vulgaris*) in the genus Caryophyllaeus. The differences as noted by Diesing (1863) were previously denoted by Wagener and subsequently by Monticelli as being specific, rather than generic. Since that date many papers have appeared dealing primarily with descriptions of various species.

The genus Archigetes was erected by Leuckart (1878) to hold a Cestodarian, "*C.*" *appendiculatus*, found by Ratzel (1868) in tubificid worms; he renames this form *Archigetes sieboldi*. Gruber (1881) describes the repro-

ductive system of *A. sieboldi*. Mrázek (1897) made a careful study of this form and added much histological and embryological data. It is unfortunately written in Hungarian, and is, therefore, inaccessible to most of the world. The same author in 1908 described another member of this genus, *A. brachyurus*, also found in the body cavity of the Tubificidae. Wisniewski (1928) briefly described a new species, *A. cryptobothrius*, from the body cavity of *Limnodrilus hoffmeisteri*.

The genus Lytocestus was erected by Cohn (1908) to hold a new Cestodarian, *L. adhaerens*. Since that date Woodland (1923, 1924) described two species which belong here, *L. filiformis* and *L. chalmersius*, as members of the genus Caryophyllaeus. The same writer (1926) refers "*C.*" *indicus* (Moghe 1925) to this genus and the "*Monobothroides*" *cunningtoni* of Furhmann and Baer (1925), as well as a form described by Johnston (1924) as "*Balanotaenia*" *bancrofti*. Nybelin (1922) in his monograph on the Pseudophyllidea reviews the literature on the Caryophyllaeidae and retains the genera Monobothrium, Caryophyllaeus, Archigetes and establishes a new one, Caryophyllaeides, to hold Schneider's "*C.*" *fennicus*. Woodland (1923) found it necessary to create the genus Wenyonia to take care of three new species, *W. virilis*, *W. acuminata* and *W. minuata*. In 1924 Kulmatycki redescribed *W. virilis* as "*Caryophyllaeus*" *noliticus*. Fuhrmann and Baer (1925) described a new genus and species which they called *Monobothroides cunningtoni*. Bovien (1926) described six new species of Caryophyllaeus, *C. javanicus*, *C. oxycephalus*, *C. serialis*, *C. tenuicollis*, *C. microcephalus* and *C. acutus*. This same author also described one new genus and species, *Djombangia penetrans*. As pointed out in a previous paper (Hunter 1929) further study of these six species will undoubtedly bring about a reclassification of these parasites which will place them in the Lytocestinae. Motomura in 1927 added another new species, *C. gotoi*. Baylis followed this in 1928 with a new genus and species, *Lytocestoides tanganyikae* which he tentatively places in the Lytocestinae.

In America progress has not been so rapid. Linton (1893, 1897) described two species of Caryophyllaeidae as "*Monobothrium*" *terebrans* and "*M.*" *hexacotyle*. Ward (1911) records the presence of Archigetes in North America and Cooper (1920) erects a new genus, Glaridacris, to hold his species, *G. catostomi*. Lamont (1921) followed this with a description of "*C.*" *laruei*. Essex and Hunter (1926), in a joint paper, record the presence of Cestodaria in various fresh water fish. Hunter (1927) published a brief redescription of the American forms and added three new genera and four new species, *Capingens singularis*, *Biacetabulum infrequens*, *Hypocaryophyllaeus paratarius* and *Monobothrium ingens*. This was followed in 1929 by the description of two new genera and five new species, *Pseudolytocestus differtus*, *Spartoides wardi*, *Glaridacris confusus*, *Biacetabulum meridianum* and *B. giganteum*.

Some of the more important general papers should be mentioned. Fraipont (1880) wrote concerning the excretory apparatus of the trematodes, cestodes and Cestodaria. In 1890 St. Remy considered certain aspects of the reproductive system of *C. laticeps* (=*C. mutabilis*). Pintner (1880) discusses the situation in the Cestodaria, and D'Udekem (1855), mentions two scolices found in Tubificidae. The homologies of the female genital organs of trematodes and cestodes were treated by Odhner (1912). Loennberg (1897) in his paper attempts to show that the Caryophyllaeidae are secondarily monozooic whereas the Gyrocotylidae are primarily so, or as he puts it, "primatively" so. This dissertation was followed in 1905 by Spengel's paper on *Die Monozootie der Cestoden*, and by Cohn (1907) on the orientation of the cestodes.

Stiles and Hassall did much to simplify the compilation of a working bibliography by their publication of the section of the Index-Catalogue of Medical and Veterinary Zoology on Subjects: Cestoda and Cestodaria.

DISCUSSION OF THE GENERA OF THE CARYOPHYLLAEIDAE

The Caryophyllaeus Group

The problem under discussion is not the old characterizations of the genera, for those have of necessity changed to keep pace with the advances in scientific knowledge, but deals with the genera proposed as valid by more recent workers. Since there may be fourteen or fifteen genera in the family Caryophyllaeidae it will be rather difficult to cope with all in detail. The genera Archigetes Leuckart 1878, Lytocestus Cohn 1908, Wenyonia Woodland 1923 appear to be accepted as valid by most workers today. The genera which will be considered are Caryophyllaeus, Monobothrium, Glaridacris and Caryophyllaeides; these have been placed by Woodland (1923, 1926) in one genus, Caryophyllaeus.

First a comparison of the characters of several of the genera considered by Nybelin (1922) will be made. He characterized the genus Caryophylaeus as follows:

> Caryophyllaeinen mit mehr oder weniger verbreitertem, dorsoventral abgeflachtem, sogar gekräuseltem Vorderende, ohne jede Spur von Saugorganen. Wassergefäss-System mit wohlausgebildeter Endblase. Vas deferens verhältnismässig stark gewunden, ohne Vesicula seminalis externa. Cirrusbeutel gross, eiförmig, Ductus ejaculatorius ohne distinkte Wandung. Mündungen von Cirrus und Ductus utero-vaginalis dicht hinter einander in einer seichten, anscheinend nicht vorstülpbaren Genitalcloake Ductus utero-vaginalis lang. Vagina mit grossem Receptaculum seminis und sehr engem, vom Receptaculum scharf abgesetztem Ductus seminalis. Germarium H-Förmig, Germiduct verhältnismässig lang, aber nicht auffallend weit, median entspringend. Uteruswindungen nie vor dem Cirrusbeutel.—Geschlechtsreif im Darm von Cypriniden. Procercoidstadium, soweit bekannt, in Tubificiden.

This is followed by the description of Monobothrium:

> Caryophyllaeinen mit trichterförmig einstülpbarem, in ausgestrecktem zustande sechskantigem, mit zwei flächenständigen, sehr schwach ausgeprägten bothrienähnlichen

Vertiefungen versehenem Vorderende. Wassergefäss-System mit wohlausgebildeter Endblase. Vas deferens verhältnismässig stark gewunden, ohne Vesicula seminalis externa. Cirrusbeutel verhältnismässig klein, birnförmig, Ductus ejaculatorius mit distinkter Wandung. Mündungen von Cirrus und Atrium utero-vaginale zusammen in einer seichten, vorstülpbaren Gentitalcloake, jedoch von eindander durch einen, die Cirrusöffnung umgebenden, voluminösen Ringwulst (männliche Genitalpapille?) ziemlich weit getrennt. Atrium utero-vaginale breit. Vagina ohne Receptaculum seminis und scharf abgesetzten Ductus seminalis. Germarium H-förmig, Germiduct verhältnismässig lang und sehr weit, nicht median, sondern rechts oder links von der Mittellinie des Germariums entspringend. Uteruswindungen nie vor dem Cirrusbeutel.—Geschlechtsreif im Darm von Cypriniden. Entwicklung unbekannt.

Nybelin creates a new genus to hold the form described by Schneider (1902). He names this genus Caryophyllaeides and characterizes it in the following words:

Caryophyllaeinen mit quer abgestumpftem, kaum merkbar verbreitertem Vorderende ohne jede Spur von Saugorganen oder Kräuselung. Wassergefäss-System mit wohlausgebildeter Endblase. Vas deferens verhältnismässig schwach gewunden, ohne Vesicula seminalis externa. Cirrusbeutel gross, eiförmig, Ductus ejaculatorius ohne distinkte Wandung. Mündung des Cirrus am inneren Ende des weiten, aber nicht besonders langen Ductus utero-vaginalis. Vagina mit wohlausgebildetem, vom Ductus seminalis aber nicht scharf abgesetztem Receptaculum seminis. Germarium mit sehr langen vorderen und dorsal sich vereinigenden hinteren Schenkeln der Seitenflügel, Germiduct kurz und sehr eng, median entspringend. Uteruswindungen zum grössten Teil vor dem Cirrusbeutel.—Geschlechtsreif im Darm von Cypriniden. Entwicklung unbekannt.

Cooper (1920) describes a fourth new genus, Glaridacris, as follows:

With the characters of the family. Medium sized caryophyllaeids with the anterior end modified to form a scolex, provided on each surface with three suckers, of which the median one is the deepest and most efficacious. Main longitudinal parenchymatous muscles in eight large fasciculi in the anterior part of the neck and the base of the scolex. Only two main nerve strands in the medulla, connected in the scolex by two more or less diffuse commissural loops. Excretory vessels form a single cortical plexus with eight principal longitudinal channels; no true flame-cells present, terminal renal organs, peculiar, highly vacuolated, simple cells. Expansion of the vas deferens before entering the cirrus-sac to form a vesicula seminalis . . . .

Woodland (1926) deletes the last three of these genera and places them in the genus "Caryophyllaeus" which he describes as:

Caryophyllaeidae with the sexual apertures situated within the last quarter of the body-length, and the ovary near the posterior extremity. The longitudinal extent of the uterus is at the most one-third of that of the testes and usually much less. Two layers of longitudinal muscles fibres, one lying external to the nuclear layer of the subcuticula and just internal to the "Stäbenschicht"—the subcuticular layer—and one separating the medullary from the cortical parenchyma—the epi-medullary layer. The vitellaia are medullary, have a more or less annular arrangement round the testes, and are in part situated behind the ovary. The ovary is in the medulla. The uterus wall is in large part invested by a thick layer of gland-cells—the uterine glands. Parasitic in the intestines of the Cyprinidae.

The question then is whether Woodland is warranted in so doing. Should these forms really be confined in one genus or was Nybelin right in maintaining Caryophyllaeus, Monobothrium and Caryophyllaeides as three distinct genera? It should be borne in mind that taxonomy at the best

is pragmatic. In the opinion of the writer it should be employed to simplify the work of classification and not to complicate it. The means of securing this end is largely a matter of personal opinion. The decision can be reached after a careful examination of the points upon which they are based. Woodland maintains his genera largely upon the position of the musculature in relation to the reproductive organs, a character undoubtedly valid, but one which is of more than generic value. Furthermore, the inner longitudinal muscles which separate the medullary from the cortical parenchyma are always readily distinguishable. The one "lying external to the nuclear layer of the subcuticula and just internal to the 'Stäbenschicht' the subcuticular layer," (called the outer longitudinal layer by this author), is not always as readily found as the former, and in fact is sometimes absent except in the neck region. It is doubtful, therefore, if this character can be used (in its entirety) with as great facility as Woodland intimates. The position of the sexual aperture and ovary is considered by both Nybelin (1922) and Lühe (1910) as a family character. The former speaks of it directly and the latter denotes the genital opening as "approaching the posterior end" and later speaks of the ovary as being behind the genital opening. It should be realized that this character would have to be altered since the description of Woodland's genus, Wenyonia, appeared in 1923, but this point will be discussed in detail later. Woodland's second character of the genus dealing with the longitudinal extent of the uterus in relation to the length of the testicular field does not hold, for the figure of "*C.*" *skrjabini* clearly shows the uterus extending longitudinally for more than one-third the length of testes. The fourth character, regarding the annular arrangement of the vitellaria is not valid for in the case of *G. hexacotyle* they are confined to two lateral rows while in *Monobothrium ingens*, Hunter (1927) there are no post-ovarian vitellaria. This merely goes to show that even Woodland's characterization of the genus Caryophyllaeus is also subject to change as other forms are described, a fact which no one could foresee and one which Woodland hoped to avoid.

Having considered Woodland's description of Caryophyllaeus we can now turn to Nybelin's. This author goes to the other extreme and includes characters which are really of specific rather than generic value. For example, the length of the utero-vaginal duct is not to be compared in value to the shape of the ovary, or the position of the uterine coils with reference to the cirrus sac. It is equally clear that several other characters, as the type and windings of the vas deferens, or the presence or absence of a distinct wall in the ductus ejaculatorius are not of generic importance. However, certain other characters as type of genital atrium, shape of ovary, position of the uterine coils in relation to the cirrus sac and the presence or absence of an external seminal vesicle are undeniably of generic import.

The same general criticism has been made by Woodland (1926) of the

genus Caryophyllaeides, the only difference being that he does not admit the existence of other characters of generic importance. A similar situation prevails with the genus Monobothrium, for here again Nybelin includes a number of characters which in the opinion of the writer are subgeneric.

There are then the two extremes, Woodland on the one hand advocating the deletion of Monobothrium, Glaridacris and Caryophyllaeides in order to secure a genus which is composed of "relatively deep-seated and easily recognizable characters, are as concise as is consistent with precision, and are not likely to require serious amendment in the near future." On the other extreme as we have seen above is Nybelin who delves deeply into the minute anatomical characters of the different species. But if the latter's characterization of the genera is fundamentally sound other species should fit into the genera already created. The description of Popoff's (1924) *"C." skrjabini* places it as another member of Nybelin's genus Caryophyllaeides, provided that some of the characters which have been termed "specific" by Woodland and this author are omitted and only the main characters retained. Such are the characters relating to the type of scolex, the presence of the inverted "A" shaped ovary, the presence of an external seminal vesicle and the position of the uterine coils anterior to the cirrus sac. There would then be two species in this genus. In a previous paper the writer (Hunter, 1927) describes a new species, *M. ingens*, which falls into the genus Monobothrium provided the same type of characters are used and the specific ones deleted. Then the genus would be characterized by the scolex, the position of the uterine coils in relation to the cirrus sac, shape of ovary, type of genital atrium, presence of an external seminal vesicle and the presence or absence of post-ovarian vitellaria. In a similar fashion two other species originally placed in Monobothrium and Caryophyllaeus respectively were shown to belong in the genus Glaridacris, these being *G. hexacotyle* and *G. laruei* (see Hunter 1927).

These examples serve to show that the genera may be retained. The question of whether a character be specific or generic is after all largely a matter of opinion. The generic characters listed above are as easily determinable as those denoted by Woodland in his description of the genus Caryophyllaeus, and the writer agrees with Woodland that they should be of such a facilely determinable nature, if possible. It seems, however, that such features could be readily distinguished by persons unacquainted with the group and therefore would have the same advantage claimed by Woodland for his classification. He says, "Above all, they possess [speaking of the genera Caryophyllaeus, etc.] the advantage that persons unacquainted with this group can, without difficulty, relegate a new or unknown species to its appropriate genus, and therefore possess the maximum of utility." As Woodland says classification is largely a matter of convenience and utility. Surely it would be simpler and infinitely easier to determine whether a spec-

ies were new by having several well defined genera each containing a few species rather than one with many. If Woodland's scheme is followed there would be 15 or 18 species in the genus Caryophyllaeus instead of three, four or more equally well defined genera with fewer species in each. Furthermore classification should primarily show relationships, setting apart those groups which differ. The genus Monobothrium was originally erected by Diesing (1863:228) to hold species which were different from those in the genus Caryophyllaeus. This group was deleted by Monticelli (1892), but later was restored, after further study of the same species, by Nybelin (1922). Once a genus has been created it should be retained if it is valid. Both Nybelin (1922) and the present author have shown its validity, and Fuhrmann and Baer (1925) as well as Meggitt (1924) have accepted Nybelin's diagnosis of the genera. The writer proposes, therefore, to retain the genera Caryophyllaeus, Monobothrium and Caryophyllaeides as well defined genera. Their characters, however, will of necessity be modified according to the preceding paragraphs.

The genus Glaridacris as described by Cooper (1920) is of little value for he makes use of characters difficult to ascertain with any degree of accuracy. It is also unsatisfactory because it does not employ the characters which are used by other workers. The difficulties are shown in the following: the first character is denoted as "With characters of the family," and might well be summed up by saying "Caryophyllaeidae"; the division of the inner longitudinal muscles into 8 fasciculi is specific rather than generic; the presence of two main nerve strands is true of all those forms which have come under my observation and probably is a family or class character; the number of main longitudinal excretory canals has been found to vary in an individual from 6, 8 to 10, or from 8, 10 to 12. The present writer also hoped to be able to make use of this character but could not. The sixth character designating the existence of renal corpuscles instead of flame cells is too difficult to be generally used. It has the further disadvantage of being a cytological rather than a morphological distinction. The characters of the scolex and the presence of an external seminal vesicle are important and of value. In other respects it closely resembles the genus Caryophyllaeus except for the fact that so far it has been found only in the Catostomidae. If this genus were retained it would hold four species. The validity of this genus may be questioned by some since its present existence depends to a large degree upon three characters, the scolex, the presence of an external seminal vesicle and the host. But upon examining the literature we find evidence of genera being retained as valid when there is only *one* distinguishing character. In the Proteocephalidae the genus Corallobothrium differs from the genus Proteocephalus in the type of scolex. To be sure, Woodland (1925) has advocated the deletion of the genus along with several others, but Essex (1928) and other workers contend that it should be retained.

Furthermore, Fuhrmann (1916) created the genus Goezeella upon the basis of the scolex alone (in which respect it differs from Monticellia). Therefore since other genera have been retained upon one character and there are here three points of difference it is evident that the genus Glaridacris should be retained as valid.

The writer has endeavored to show in the preceding paragraphs that the following genera should be retained: Caryophyllaeus, Monobothrium, Glaridacris, Caryophyllaeides and three which were not discussed, Archigetes, Lytocestus and Wenyonia. The first four may be characterized by type of scolex; type of genital atrium, (i. e. whether the cirrus opens into the utero-vaginal canal, or whether there are two separate orifices etc.); shape and position of ovary (whether medullary or cortical); position of uterine coils in relation to cirrus sac; presence of post-ovarian vitellaria; position of vitellaria in relation to inner and outer longitudinal muscles; the presence or absence of an external seminal vesicle; host.

The genus Archigetes is described by Nybelin (1922:134) as follows:

> Caryophyllaeinen mit verjüngtem und dorsoventral abgeflachtem oder sechskantigem, stets aber mit zwei flächenständigen, anscheinend gut ausgeprägten, bothrienähnlichen Vertiefungen versehenem Vorderende. Wassergefäss-System nicht mit einer einzigen Endblase, sondern mit zahlreichen Ampullen am Hinterende des Körpers. Vas deferens sehr schwach gewunden, mit birnförmiger Vesicula seminalis externa. Cirrusbeutel verhältnismässig klein, rundlich, Ductus ejaculatorius mit distinkter Wandung. Cirrus in den Ductus utero-vaginalis mündend. Vagina ohne oder mit nur schwach differenziertem Receptaculum seminis und Ductus seminalis. Germarium hantelförmig, Germiduct median entspringend. Uteruswindungen wenig zahlreich, zum kleineren Teil auch vor dem Cirrusbeutel.—Geschlechtsreif mit zeitlebens erhaltenem, die Embryonalhäkchen tragendem Schwanzanhang in der Leibeshöhle von Tubificiden.

Undoubtedly a more detailed study of this group will disclose several new genera. However, the generic characterization remains broader if the cirrus sac, ductus ejaculatorius and the oviducal characters are omitted. The others are valid, but in the opinion of the writer, are specific rather than generic in character.

The Lytocestus Group

The genus Lytocestus is described by Cohn (1908:139) in these words:

> Scolex unbekannt. Frühe Loslösung der Proglottiden, keine Differenzierung an deren Haftende. Keine präformierte Uterusöffnung; ♂ und ♀. Genitalporus hintereinander, flächenständig. Hoden zahlreich in der Markschicht; Ovarium zweiteilig mit medianem Reservoir, Dotterstöcke in der Rindenschicht, ringförmig, Schalendrüse neben dem Ovarialreservoir. Im Darme von Fischen.

Later Woodland (1926: 56) describes the genus as:

> Caryophyllaeidae in which the position of the sexual apertures and ovary and the relative longitudinal extents of the uterus and testes are as in *Caryophyllaeus*. The longitudinal muscles consist of two layers, as in *Caryophyllaeus*, but the outer layer (the cortical layer) is internal to the nuclear layer of the subcuticula and not external to it. The vitellaria are

cortical, have an annular arrangement round the testes, and are wholly absent behind the ovary. The follicles of the ovary are cortical, only the median receptacle and the proximal portions of ducts being medullary. Uterine glands present. Parasitic in intestines of Mormyridae and Siluridae."

In the light of our present knowledge it is apparent that Woodland's (1926) description of the genus goes to the same extreme as does his characterization of Caryophyllaeus. This raises the question of whether or not he is using characters which are of greater than generic value. Cohn (1908), although his description is inadequate, goes into too much detail and like Nybelin, uses subgeneric characters. The genus Lytocestus can be maintained on the basis of scolex character, type of the male and female genital pores, presence or absence of post-ovarian vitellaria, relation of the longitudinal extent of the uterus to that of the testes, shape of the ovary and the host. This leaves many of Woodland's (1926) characters unused. The reasons for this will appear in subsequent paragraphs.

Fuhrmann and Baer (1925) describe a new species of Cestodarian which they place in a new genus and species, *Monobothroides cunningtoni*. Certainly it is related to the genus Lytocestus and according to Woodland it should be considered as a synonym of this genus. However, in this author's revision of Lytocestus the genus Monobothroides differs from it primarily in the type of scolex. This character alone is perhaps sufficient grounds for maintaining the genus, but before the question can be definitely settled the writer feels that the original description of Cohn's (1908) *L. adhaerens* should be amplified. Inasmuch as Monobothroides is probably valid it should be left as a genus until it is definitely proved to belong elsewhere, and if further study shows the genus to be valid, the author believes that *L. chalmersius* may be found also to belong in the genus Monobothroides.

The Wenyonia Group

The genus Wenyonia was added to the Caryophyllaeidae in 1923 when it was originally tersely described by Woodland (1923:455) in these words:

> The sexual apertures situated in the anterior half of the body. The longitudinal extent of the uterus is at least equal to that of the testes. Parasitic in the intestine of Siluridae.

Three years later (1926:59) the definition was amplified so that it read:

> Caryophyllaeidae in which the sexual apertures are situated in the anterior half of the body. The longitudinal extent of the uterus is at least equal to that of the testes. The longitudinal muscles may consist either of one thick layer occupying the whole cortex, or this may become split into two layers resembling those of Lytocestus. The vitellaria are medullary, are restricted in position to two lateral narrow tracts, and extend behind the ovary. The entire ovary is medullary. Uterine glands are absent. Parasitic in the intestines of Siluridae.

It is the belief of the author that a subsequent study of this group will make it possible to make more use of the same type of characters so typical of the Caryophyllaeus group. However, for the present the genus may be

characterized by scolex, longitudinal extent of the uterus, position, shape and type of the ovary, non-reduced ovarian commissure, presence of a terminal excretory bladder and the host.

The writer has attempted to show that the three groups of Caryophyllaeidae are distinct and yet are warranted in being subdivided into more than the one genus proposed by Woodland (1926). It is evident, however, from Woodland's account and figures that these three "genera" are fundamentally different. Yet Nybelin, Fuhrmann and Baer and the present writer have all pointed out how these groups may be subdivided into their respective valid genera. Furthermore, the genera in the Caryophyllaeus group, Caryophyllaeus, Monobothrium, Glaridacris, Caryophyllaeides and Archigetes, are undeniably more closely related to each other than to such forms as Lytocestus and Wenyonia. For example, both Monobothrium and Caryophyllaeus have vitellaria which are medullary and surrounded by the inner longitudinal muscles, their sexual apertures are within the last quarter of the body length, and uterine glands are present. They conform, in other words, to some of Woodland's characters, but they differ from Lytocestus in the location of the vitellaria in relation to the inner longitudinal muscles. These two genera differ markedly from Lytocestus and yet are fairly close to Woodland's definition of Caryophyllaeus. Since classification is meant to show relationships and a study of this group has shown the existence of the Caryophyllaeus, Lytocestus and Wenyonia groups, which have been sensed by Woodland (1926:63) when he says "that the three genera—Caryophyllaeus, Lytocestus, and Wenyonia—above defined by me are as distinct from each other as are any three genera contained in any other family of the Cestoda,"—the writer (1927) erected three subfamilies, the Caryophyllaeinae, Lytocestinae and Wenyoninae to hold the three groups of related genera.

The family Caryophyllaeidae would then be retained as the only family of the monozootic Pseudophyllidea, which in turn would contain Nybelin's (1922) subfamily Caryophyllaeinae (=Caryophyllaeidae Lühe) with modified characters, and the two new subfamilies, Lytocestinae and Wenyoninae. A brief account was published in 1927. This necessitates taking the subfamily Caryophyllaeinae of Nybelin (which is equal to the family Caryophyllaeidae of Lühe (1910)) out of the family Cyathocephalidae and placing it back by itself as a family of monozootic Pseudophyllidea.

THE CAPINGENS GROUPS

During the preparation of this monograph several genera were found which clearly belonged to still another group. The genus Capingens described by the author in 1927 was placed in the Lytocestinae on the basis of the relation of the musculature to the vitellaria. It was noted at the time that the vitellaria were not *entirely* cortical to the inner longitudinal muscles,

but instead had their origin within the muscle band (i. e. medullary) and extended through the inner longitudinal muscles into the cortical layer. This was interpreted at the time as being sufficient grounds to place it with the Lytocestinae. Recently the author has discovered two more genera, Pseudolytocestus and Spartoides, which possess this same arrangement of the vitellaria. These three genera are clearly alike in this important respect, and the author therefore placed them in a new subfamily, the Pseudolytocestinae (Hunter 1929). Attention has been called to the necessity of changing the subfamily designation from Pseudolytocestinae to Capingentinae since Capingens was picked as the type genus.* There are now four subfamilies of the Caryophyllaeidae; the Caryophyllaeinae, Capingentinae, (=Pseudolytocestinae), Lytocestinae and Wenyoninae.

Phylogenetically the Caryophyllaeidae are undoubtedly closely allied to the bothriocephalid tapeworms. This is shown more clearly than ever by the new genera which were described by the author in 1927. Both the genus Capingens and Biacetabulum have type species whose scolices clearly resemble the bothria and acetabular types respectively. The morphological details of the musculature are likewise remarkably similar, an indication that the groups are closely allied. The final word, however, must be withheld until such time as the life histories of these parasites are worked out.

KEY TO THE GENERA OF THE CARYOPHYLLAEIDAE

1 (37) Caryophyllaeidae with sexual apertures and ovary situated in last fourth of body length.......... 2

2 (18) Vitellaria entirely medullary..........Caryophyllaeinae 3

3 (12) Caryophyllaeinae with uterine coils extending anterior to the cirrus sac.......... 4

4 (10) Adults parasitic in fish.......... 5

5 (7) Ovary not "H" shaped.......... 6

6 Ovary shaped like inverted "A;" scolex undifferentiated; cirrus sac opens into utero-vaginal canal..........Caryophyllaeides

7 (5) Ovary "H" shaped.......... 8

8 (9) Scolex well defined, bearing one pair acetabular-like suckers; external seminal vesicle present..........Biacetabulum.

9 (8) Scolex poorly defined, bearing three pairs of loculi; cirrus opens on ventral surface or into a shallow atrium ahead of the female; external seminal vesicle present ....Hypocaryophyllaeus.

10 (4) Adults parasitic in body cavity of Tubificidae.......... 11

11 Caudal vesicle bearing embryonic hooks..........Archigetes.

12 (3) Caryophyllaeinae with coils of uterus never extending anterior to cirrus sac.... 13

13 (15) Scolex with terminal introvert.......... 14

* Dr T. Harvey Johnston, The University, Adelaide, Australia kindly brought this matter to my attention.

14 Scolex hexagonal, with terminal introvert; 6 weak shallow grooves; cirrus and utero-vaginal canal open together in last fourth body length into a shallow evertible cloaca separated by bulky annular pad (male papilla?). Monobothrium.

15 (13) Scolex without terminal introvert.. 16

16 (17) Scolex with anterior extremity broadened or curled, not specialized into loculi, bothria, etc.; cirrus opens on ventral surface or into shallow non eversible atrium; no external seminal vesicle present.........................Caryophyllaeus.

17 (16) Scolex well defined with 3 pairs of loculi or suckers; external seminal vesicle present...Glaridacris.

18 (2) Vitellaria not entirely medullary, but entirely cortical or partly cortical........ 19

19 (31) Vitellaria entirely cortical, lying external to the inner longitudinal muscle layer..Lytocestinae 20

20 (22) Inner longitudinal muscle mass arranged in two parallel sheets between testes.. 21

21 Lytocestinae with scolex possessing longitudinal loculi and distinct muscular "frill;" uterine coils do not extend anteriorly to cirrus sac and reach a maximum length of less than one-half that of testicular field...............Balanotaenia.

22 (20) Inner longitudinal muscles annularly arranged about testes.................. 23

23 (26) Scolex devoid of specialization.. 24

24 (25) Lytocestinae with no post-ovarian vitellaria; uterine coils extend anterior to wings of ovary..Lytocestus.

25 (24) Lytocestinae with vitellaria continuous laterally with post-ovarian group; uterine coils do not extend anterior to ovarian wings............Lytocestoides.

26 (23) Scolex specialized (i.e. bears loculi, bothria, etc.).......................... 27

27 (29) Uterine coils extend anteriorly nearly as far as testes........................ 28

28 Lytocestinae with globular scolex armed with terminal sucker; uterine coils divide testicular field in half; post-ovarian vitellaria absent.......Djombangia.

29 (27) Uterine coils extend anteriorly less than one-half the length of testicular field.. 30

30 Lytocestinae with scolex bearing longitudinal furrows and terminal introvert; uterine coils never extend beyond anterior wings of ovary; post-ovarian vitellaria absent...Monobothroides.

31 (19) Vitellaria not entirely cortical, but having a medullary origin and extruding one third to one half (or more) into cortical parenchyma...Capingentinae (=Pseudolytocestinae) 32

32 (34) Scolex occupying one-fifth or more of entire body length.................... 33

33 Capingentinae with scolex bearing one pair of large bothroid suckers; post-ovarian vitellaria present.......................................Capingens.

34 (32) Scolex occupying less than one-fourth or one-fifth of body length............. 35

35 (36) Capingentinae possessing "U" shaped ovary with cirrus sac lying within wings of ovary; external seminal vesicle present; no post-ovarian vitellaria present. ....Spartoides.

36 (35) Capingentinae possessing undifferentiated scolex and "H" shaped ovary; no post-ovarian vitellaria; prominent external seminal vesicle..Pseudolytocestus.

37 (1) Caryophyllaeidae with sexual apertures in anterior half of body length.. Wenyoninae 38

38 Longitudinal extent of uterus at least equal to that of testes; parasitic in Siluridae ....Wenyonia

FAMILY CARYOPHYLLAEIDAE LEUCKART 1878

Family diagnosis: Pseudophyllideans with or without organs of adhesion on scolex. Ovary and genital openings present singly, lying on ventral surface. Testes exclusively confined to medullary parenchyma; vas deferens located anteriorly to thick, muscular cirrus sac. Oviduct arises from oöcapt with origin in ovarian commissure. Utero-vaginal duct without sphincter. Two main longitudinal nerve strands are present.

SUBFAMILY CARYOPHYLLAEINAE (Nybelin, 1922)

Subfamily diagnosis: Caryophyllaeidae with sexual apertures and ovary situated within last quarter of body length. Longitudinal muscles usually consist of two layers, inner always surrounding vitellaria which are medullary and typically annularly arranged. Uterine glands present.

Type genus: Caryophyllaeus Müller 1787.

GENUS CARYOPHYLLAEUS O. F. MÜLLER 1787

Generic diagnosis: Caryophyllaeinae with broadened, folded or "curled" anterior extremity not specialized into loculi, bothria or suckers. Cirrus opens on ventral surface or into shallow non-eversible genital atrium. Medullary ovary "H" shaped. Uterine coils never extend anterior to cirrus sac, with maximum length one-third that of testicular field, usually less. No external seminal vesicle; post-ovarian vitellaria and terminal excretory bladder present. Parasitic in digestive tract of Cyprinidae and Catostomidae. Development unknown; procercoid stage supposed to occur in body cavity of Tubificidae.

Type species: *Caryophyllaeus laticeps* (Pallas 1781). To include:

(1) *C. laticeps* (Pallas 1781) (=*C. mutabilis* Rud. 1802)
(2) *C. syrdarjensis* Skrjabin 1913
(3) *C. armeniacus* Cholodkowsky 1915
(4) *C. caspicus* Klopina 1919
(5) *C. fimbriceps* Klopina 1919
(6) *C. terebrans* (Linton 1893)
(7) *C. gotoi* Motomura 1927
(8) *C. javanicus* Bovien 1926
(9) *C. oxycephalus* Bovien 1926
(10) *C. serialis* Bovien 1926
(11) *C. tenuicollis* Bovien 1926
(12) *C. microcephalus* Bovien 1926
(13) *C. acutus* Bovien 1926

It is very probable that the six species described by Bovien (1926) will be placed in other genera after further study. Bovien realized this when he said "No doubt the genus Caryophyllaeus in the rather wide sense

adopted in my paper shall have to be divided, but considering the rapid increase in the number of species, I prefer to wait." These six species are all found in members of the Siluridae which is one of the characteristics of the Lytocestinae. Furthermore, none of Bovien's species possess post-ovarian vitellaria which is more typical of the Lytocestinae than the Caryophyllaeinae. It is, of course, impossible to determine their true position without further study, as there are no figures of sectioned material.

CARYOPHYLLAEUS TEREBRANS (LINTON 1893) Char. emend.

[Figs. 1, 30, 31, 51, 72]

1893: *Monobothrium terebrans*	Linton	1893: 545–564
1922: "*Monobothrium*" *terebrans*	Nybelin	1922: 123–124
1923: *Caryophyllaeus terebrans*	Woodland	1923: 450–460
1927: *Caryophyllaeus terebrans*	Hunter	1927: 18

Specific diagnosis: With characters of genus. Adult parasites measuring 5 to 30 mm. in length and 0.8 to 2.5 mm. in width frequently embedded in the intestinal wall. Neck distinct, slightly narrower than dorso-ventrally flattened body. Cuticula 5 to 10 μ thick; subcuticula 6 to 15 μ thick, followed by cortical parenchyma 50 to 75 μ in depth. Inner and outer longitudinal muscles present and equally prominent. Testes nearly spherical, numbering 175 to 225 in normal adults, with maximum diameter from 0.15 to 0.27 mm. Ovoid to round cirrus sac occupies one-third to one-half of medullary parenchyma; diameter varying between 0.2 and 0.45 mm.; circular muscles from 12 to 19 μ in thickness. Inner band of circular muscles forms inner cirrus sac varying between 0.2 and 0.27 mm. Male and female reproductive systems open on surface 0.09 to 0.2 mm. apart. Vagina median, ventral, convoluted, not forming receptaculum seminis. Length of ovarian wing, varies between 0.6 and 1.15 mm. by 0.13 to 0.3 mm. Maximum diameter of vitellaria 0.228 mm. Eggs ovoid 55 to 65 by 30 to 36 μ.

Host: *Catostomus ardens*, Heart Lake, Yellowstone National Park, Wyoming; *Ictiobus bubalus*, Tallahatchie River, Money, Mississippi. In intestine.

Paratype: Linton's original slides, two in number (233/1) loaned to Prof. H. B. Ward, University of Illinois, Urbana, Illinois.

Bottled material in author's collection No. 645.

Host	Locality	Collector	Authority
Catostomus ardens Jordan and Gilbert	Heart Lake, Yellowstone Nat'l. Pk., Wyo.	E. Linton	Linton 1893: 545–564
Ictiobus bubalus (Rafinesque)	Tallahatchie River, Money, Miss.	Parke H. Simer	Hunter (the present paper)

This species has the distinction of being the first Cestodarian parasite to be recorded from North America. Dr. Edwin Linton secured the material from the intestine of *Catostomus ardens*. The fish were taken on July 28, 1890 by a trammel net in Heart Lake, Yellowstone National Park. The revised description of this species is based upon the original paper of Linton (1893), upon some of his original slides and some of the same species collected from *Ictiobus bubalus* in the spring of 1927 by Dr. Parke H. Simer near Money, Mississippi.

The original description was based largely upon contracted forms. One of the slides loaned to Professor Henry B. Ward was a sexually mature specimen measuring but 5 mm. long whereas no mature forms collected by Dr. Simer were under 20 mm. in length. The minimum measurements therefore will be based upon Dr. Linton's slides and the maximum upon the normally contracted forms in the author's collection.

The parasites range between 5 and 30 mm. in length. Sexually mature parasites appeared from 20 mm. and up in cases of normal contraction. The scolex typically is bluntly rounded or cone shaped, and tapers into a neck, the narrowest part of the body (Fig. 1). In cross section the neck is round although posteriorly the body is oval. *C. terebrans* is much wider proportionately than any other parasite described. It possesses a width of 0.8 to 2.5 mm. The latter figure is cited by Linton as the breadth of a specimen 17 mm. long. In highly contracted forms the maximum width occurs at the base of the scolex just before it passes into the neck.

The parasites were not found originally in any considerable numbers; only twelve being taken from two fish. Some were embedded in the intestinal wall in pits, frequently several being found in the same cavity. One specimen was described by Linton (1693: 548) as follows: "Upon examining the alocholic specimens one was found 7 mm. in length, which was wholly inclosed in a pit in the mucous membrane. The walls of the pit were thick and gristly and the head end of the parasite had nearly perforated the intestinal wall." None of the specimens secured from Mississippi showed this characteristic.

The scolex of this species is perfectly smooth and bears no suckers or loculi. The slides as well as the original description substantiate this. The general shape of the head, as described by Linton is "variable, subsagittate, wedge shaped or bluntly rounded, a little broadened and thicker than the body, somewhat depressed dorso-ventrally—." A frontal section of the scolex shows the presence of a great number of longitudinal muscle fibers from the inner longitudinal system. All of these fibers extend to the distal portion of the scolex where they disappear in the subcuticula and basement membrane. It is evident, as in other forms, that these muscle fibers are inserted on the latter structure. The outer longitudinal muscles as reported by Linton (1893:550) do not show in sagittal sections but are

very evident in material from the author's collection which has been cross sectioned (Fig. 72). Cross muscle fibers are found in considerable numbers in the scolex; these extend both in a lateral as well as a dorso-ventral plane.

The entire scolex is composed of a spongy matrix of parenchymatous tissue. Here are found the canals of the excretory system. The canaliculi of the ascending system were traced in considerable numbers to the distal parts of the scolex. It is probable that these canals aid in the elongation of the scolex. It is easy to conceive that the fluids of the excretory system if forced to the anterior end would fill the canals and canaliculi and thereby cause the protrusion of the scolex. Such an extension could not occur without the aid of some of the muscles of that region, the presence of the cross fibers of the scolex suggesting that such fibers prevent the lateral expansion of the scolex and thereby aid in the anterior extension of the scolex. Retraction of the scolex is readily accomplished by the contraction of the large inner longitudinal muscles.

There is one other peculiarity of this scolex. Here, as in the case of *Monobothrium ingens*, the posterior central portions of the scolex contain numerous bodies staining readily with eosin. In the latter case, however, these bodies are confined laterally by the inner longitudinal muscles and in the former are restricted only to the cortical and medullary parenchymal regions; in the material of *C. terebrans* at hand the two are inseparable. These bodies are nucleate and filled with globules and are irregular in shape. It was impossible to definitely trace them to the excretory system and so far it has been equally impossible to connect them with any other organ system. They may be excretory products secreted through the activity of the scolex which are later to be dissolved, resorbed and carried off by the excretory system. Or, they may be glandular cells concerned with the penetration of the parasite through the mucosa of the intestines.

The integument is composed of the cuticula, basement membrane and the cuticular muscles, circular and longitudinal. In Linton's specimens the cuticula is very thick, measuring 10 to 16 μ, the lower 0.8 to 1 μ being distinguishable as the basement membrane. In older specimens the cuticula is vacuolated reminding one of the descriptions of the foramina secondaria noted by Fraipont (1881), except that they do not open to the outside. These vacuoles usually circular are irregular in shape, the largest measure 3μ in length. They lie in the middle of the cuticula which appears smooth on the outer surface and is bounded medianly by the basement membrane. Within these two smooth areas lies the vacuolated portion of the cuticula. The granules appear to be situated in a reticulum composed of fine canaliculi. This may have been caused by poor fixation or possibly by a partial breakdown of the cuticula. In the material collected in 1927 the

cuticula varied between 5 and 7μ in thickness and showed no such characteristics.

The cuticular muscles are beneath the basement membrane. The outer circular muscles are less than 0.8 μ in thickness. The longitudinal cuticular muscles, on the other hand, are nearly twice as thick, measuring from 1 to 3 μ. These two sets of muscles are situated at the outermost edge of the dense nucleate layer of the subcuticula. This layer extends medianly to the outer longitudinal muscle band 15 to 33 μ from the edge of the cuticula. These muscles mark the end of the subcuticula and separate it from the cortical parenchyma. Normally most of the subcuticular cells are found within the confines of the subcuticula. In this species, however, the cortical parenchyma is just about as densely packed with parenchymal cells as is the subcuticular layer. The presence of the canals of the excretory system in the cortical parenchyma is the one character which distinguishes the two. The reproductive organs nearly fill the medullary parenchyma with its scattered parenchymal cells.

The muscular system, as in other members of the Caryophyllaeinae, is divided into two portions, the cuticular and the parenchymal. The former has been described in detail in the preceding paragraphs and will not be reconsidered. The parenchymal muscle system appeared well developed in one of Linton's slides. It extends into the posterior third of the body as a distinct layer whose position varies between 15 to 33 μ from the exterior. This great range is caused by the outer longitudinal muscles being pushed outward, as the uterus becomes distended with eggs. These muscles extend anteriorly into the scolex and pass to the mid-lateral region where they become attached.

The inner longitudinal muscles lie 60 to 95 μ from the outer edge of the cuticula and extend from the posterior tip to the distal end of the scolex where the fibers break up to become inserted in the basement membrane. After the neck is passed these fibers arrange themselves as a definite sheath about the vitellaria which in turn nearly surround the testes (Fig.72). The fibers of this muscle layer extend to the posterior tip of the body where they are not inserted on the basement membrane, but form a continuous sheath about the post-ovarian vitellaria. The continuity of these fibers is broken ventrally by the cirrus sac. A few are inserted posteriorly on the excretory bladder. One of the slides studied was a frontal section of an adult which had contracted to 5 mm. in length. In this specimen the inner longitudinal muscles assumed their natural position just as the anterior testes were reached 1.2 mm. from the distal tip of the scolex.

The dorso-ventral as well as the lateral muscle fibers are abundant, especially in the medullary parenchyma; the diagonal muscle fibers, however, are limited. Specialized muscles appear in the scolex where the longitudinal layer of cuticular muscles become converted into the small transverse

fibers which permeate this region. It is probable that their origin is the same as those described for *Biacetabulum infrequens*, *Capingens singularis*, etc. Other specialized muscles will be described in connection with the systems in which they occur.

The major portions of the excretory system are found between the inner and the outer bands of longitudinal muscles. These paired canals extend from the anterior portions of the scolex where they are found scattered throughout the cortical and medullary parenchyma to the posterior extremity. At this point they empty into the excretory vesicle described by Linton (1893: 550) as follows:

"A terminal pore leading into a short duct with thick walls was observed in transverse sections through the posterior end of a small specimen. The duct enters posteriorly from near one margin and not from the extreme tip, and continues anteriorly to the posterior vitelline gland. The same was observed in transverse sections of larger specimens, where it appeared first in the posterior sections as a pore entering one of the margins, and was soon seen, in succeeding anterior sections, toward the middle of the sections as an elongated opening with strong walls of connective tissue of irregular thickness. In the smaller specimens strong connective fibers run from the anterior end of this cul-de-sac. This organ is doubtless the terminal pulsating organ common to larval cestodes."

This description is adequate. Ten pairs of main excretory canals were present, although their number was increased in the anterior end where they broke up into numerous canaliculi of the ascending system (Fig. 72). These extend to the distal portion of the scolex. As has already been described in the paragraphs dealing with the scolex these canaliculi when filled with the products of the excretory system become turgid and aided by the transverse muscle fibers, cause the elongation of the scolex. This is in accord with the phenomena observed in living specimens of other species.

The testes are found within the inner longitudinal muscle layer almost completely surrounded by the vitellaria. In young specimens the testes begin about the anterior third or fourth of the body. Actual count of the number of testes in Linton's specimen was 81. The other slide loaned by him, a section of the posterior region, indicated the presence of considerably more. A check made upon the material secured in 1927 indicates a close correlation with the original except in the matter of the testes count. This was found to be between 175 and 225. The arrangement and size of all structures are essentially identical in the slide of the posterior region and my own material, clearly pointing to the identity of the forms. The only apparent explanation is two fold, either Linton had representatives of two species or that one matured unusually early before the male reproductive system had completed its development, the reverse of the normal con-

dition. The latter explanation has been accepted by the author. The true testes count based upon a study of three sexually mature adults clearly places the number between 175 and 225. In sections they appear irregularly ovoid in shape, ranging between 0.13 to 0.27 mm. long and 0.09 to 0.16 mm. wide (Fig. 72).

No connection could be demonstrated between the vas deferens and the testes which lie in a dorsal and ventral row between the lateral rows of the vitellaria. These have the appearance of surrounding the testes for they are intermingled between them in all except the lateral region. The usual arrangement is an alternation of testes and vitellaria (Fig. 72). As in the case of the other species studied the vas deferens lies close to the testes and even appears to bend towards first one and then another testis. The vas deferens descends posteriorly from a median position and enters the portion of the medullary parenchyma anterior to the cirrus sac. This region is devoid of testes and vitellaria. The vas deferens is thin-walled and passes ventrally into a convoluted region between 0.15 and 0.67 mm. in length. The entire region occupied by the vas deferens is triangular with the base against the anterior side of the cirrus sac. It is swollen and filled with spermatozoa. The maximum diameter of the expanded tube varies between 84 and 120 μ. The convolutions of the vas deferens pass dorsally and enter the muscular ductus ejaculatorius the diameter of which is between 30 and 54 μ. The lining of this tube is characteristic of the seminal vesicle and the cirrus sac. The thin walls of the vas deferens are supplanted by a thicker membrane which in turn is surrounded by a wall of circular muscles 18 to 28 μ in thickness. The ductus ejaculatorius does not form a characteristic seminal vesicle; Linton in his original description neither mentions this, nor figures it, and the slides at my disposal do not show the presence of a true external seminal vesicle. Neither is the distal portion of the cirrus sac modified to form an internal seminal vesicle. The ductus ejaculatorius is convoluted, extending to the anterior median, lateral wall of the cirrus sac where it becomes surrounded by some of the muscles of the cirrus sac. It extends to the dorsal surface where it penetrates the remaining layers of the muscles to the innermost portions of the cirrus sac proper (Fig. 30, 31).

The circular cirrus sac is penetrated from the dorsal surface, slightly posterior to the center (Figs. 30, 51). As the cirrus itself is retracted, the tubules of the sac are closely coiled in the dorsal portion. The cirrus sac occupies about one third to one half of the medullary parenchyma and measures 0.2 to 0.45 mm. in greatest diameter. There appear to be two layers of circular muscles which compose the cirrus sac as a whole. The inner circle of muscles which varies between 0.2 and 0.27 mm. surrounds the cirrus sac proper. This checks with Linton's original material which measures 0.14 to 0.2 mm. The circular muscles of the outer and inner

regions of the cirrus sac are 25 to 31 μ and 8 to 15 μ respectively. The outer layer functions in the retraction of the cirrus. Linton (1893: 551) reports finding all the cirri retracted. The cirrus aperture, as seen in section is irregular and shows "puckered walls." The long axis of this aperture lies transversely to the long axis of the body. (Fig. 30.)

The vitellaria are described by Linton (1893:551) as consisting of "two marginal glands which connect with a posterior gland lying behind the ovary. In the adult specimens this organ may be divided into at least three distinct glands, one posterior and two marginal." These observations coincide with my material with but one exception. The irregularly rectangular vitellaria extend as a band and nearly surround the testes. They pass laterally and posteriorly as far as the cirrus sac. In sections their measurements vary between 0.05 and 0.22 mm. in length and 0.016 to 0.076 mm. in width. Linton (1893:551) describes the vitelline ducts as sometimes being crowded with small globular masses. This condition is typical of vitelline ducts. He neglects to mention the number and distribution of these ducts, other than note that they connect with the oviduct near the dorsal posterior edge of the ovarian commissure (germ gland). Linton's figures indicate the presence of 6 vitelline ducts, three from each side. The anterior one comes from the marginal anterior vitelline glands and unites with the oviduct (germ duct). According to Linton's figures the combined ducts pass posteriorly where they are joined from the sides by the other two vitelline ducts from the post-ovarian vitellaria. These in turn are supposedly composed of two ducts, one from the median portion of the post-ovarian vitellaria and one from the lateral. My material, however, shows clearly the presence of single vitelline ducts uniting with the oviduct. The anterior vitelline ducts first appear median to the outer row of the vitellaria and anterior to the vas deferens and the uterus. This canal passes laterally to a position just within the inner longitudinal muscles and between them and the expanded uterine coils. As the ovary is reached the vitelline ducts again turn medianly and slightly ventrally so as to pass beneath and on the inside of the main ovarian wings. As the ovarian commissure is passed the vitelline ducts pass medianly and are joined by similar canals which originate from the most anterior portion of the post-ovarian vitellaria. This common vitelline duct continues medianly along the posterior edge of the commissure until nearly in the center of the parasite. It then turns posteriorly, to the right, and sometimes expands to form a vitelline reservoir. The oötype lies close beside it and the vaginal-oviducal canal (fertilization chamber) is joined by this common vitelline duct before the center of the oötype is reached (Fig. 51).

Globular lobate ovary is situated near the ventral surface and possesses the characteristic "H" shape. Its length measures between 0.6

and 1.15 mm. and the width varies between 0.13 and 0.30 mm. The ovarian commissure the median portion of which serves as an ovarian reservior has a maximum diameter of 0.3 mm. The wings of the ovary extend posteriorly to the vitelline mass at the posterior tip of the body, and anteriorly until they reach the uterine coils. Linton (1893:551) reports the degeneration of the ovarian commissure when the uterus is filled with developing embryos. None of the material studied by the writer showed this characteristic.

The oöcapt arises from the ovarian commissure on the median posterior side. The sphincter muscle controlling the release of eggs is small, as is the canal. The oviduct takes its origin from the distal end of the oöcapt which is situated on the posterior edge of the ovarian commissure. The tube is 4 to 6 μ in diameter and is surrounded by a layer of cells which surrounds the cuticula-like lining and in its turn is covered by a layer of circular muscles 7 to 9 μ thick. The total diameter of the tube, including the lining cells, is 27 to 33 μ. The oviduct passes posteriorly for 50 to 75 μ where it is joined by the vagina. This duct arises anteriorly from the posterior margin of the female utero-vaginal canal cloaca, passes posteriorly near to the middle of the body. The course of the vagina is rather tortuous for it is pushed this way and that by the distended, egg-filled uterus. As the ovarian commissure is approached the vagina swings dorsally and passes over it, then drops ventrally and unites with the oviduct. It was not possible to demonstrate a receptaculum seminis such as Linton (1893:552) described. The width of the vagina is nearly constant having a diameter of 36 to 40 μ. The walls are surrounded by a thin layer of circular muscles.

As already described, the vagina meets the oviduct 50 to 75 μ from the origin of the latter. This combined oviducal-vaginal canal (fertilization chamber) passes posteriorly and towards the right side where it enters the oötype complex. The vitelline ducts which have now united in a single duct, and have become swollen and convoluted, functioning as a reservoir, join the combined vaginal-oviducal canal to form the beginning of the uterus. The uterus passes through several convolutions within the oötype. It then winds posteriorly into the thin walled portion which lies between the ovarian commissure and the post-ovarian vitellaria. The uterine canal proceeds dorsally and medianly, passes anteriorly over the ovarian commissure and between the wings of the ovary. This convoluted canal continues, never passing anterior to the cirrus sac, until it finally dips ventrally and empties to the ventral surface 0.09 to 0.2 mm. behind the cirrus sac. The vagina empties into this common female cloaca from the posterior side as already described (Fig. 30). The pores of the male and female systems are therefore separated and do not open into a common genital atrium, but lie 0.09 to 0.2 mm. from each other.

The eggs of this species were nearly all contracted out of shape so that accurate measurements were difficult to secure. They are ovoid and as far as it was possible to determine, non-operculate. The size ranges between 58 and 65 μ in length and 29 to 35 μ in breadth. This essentially substantiates the measurements given by Linton. The shell is 1.5 to 2.1 μ in thickness. The globular masses within the shell are about 10.5 μ in diameter.

C. terebrans was recorded originally from *Catostomus ardens*, but has since been found in *I. bubalus*.

The lack of specialization of the scolex coupled with the absence of an external seminal vesicle places this form in the genus Caryophyllaeus. *C. terebrans* was the first Cestodarian to be recorded from this continent; it also was the first record of this group of parasites from fish of the family Catostomidae. There are three other species of the Caryophyllaeidae which are known to occur in the same genus, Catostomus. The dearth of suckers or loculi distinguishes *C. terebrans* from all the members of the genus except *C. laticeps*, *C. syrdarjensis*, *C. armeniacus* and *C. gotoi*. The first two and the last possess scolices which are broader at the apex and not conical as in *C. terebrans*. *C. syrdarjensis* is further demarked by the presence of four longitudinal rows of "Fäserzellenstränge" and in shape and position of the cirrus sac. *C. gotoi* recorded by Motomura (1927) appears to have been inadequately described. It differs from *C. terebrans* in body length, shape of the scolex, number of testes (being only 30 to 40) and the presence of a receptaculum seminis. In addition it is recorded from a new host, *Misgurnus anguillicaudatus*. *C. laticeps* also differs from *C. terebrans* in the number of testes, 350 to 400, which was checked by Nybelin's (1922:126) count of 366. This difference coupled with the presence of a receptaculum seminis, type, angle, and size of the cirrus sac, length of the female genital atrium, and length of the ovary, clearly separates *C. laticeps* from *C. terebrans*. The description of *C. armeniacus* is inadequate, but the greater length and breadth, 55 mm. and 5 mm. respectively, the absence of post-ovarian vitellaria and the immense eggs eliminates the possibility of *C. armeniacus* being a synonym of *C. terebrans*. The two species described by Klopina (1919), *C. caspicus* and *C. fimbriceps* differ from *C. terebrans* in the type of scolex which is broadened and "curled" in both cases and also both her species are characterized by rows of "Fäserzellenstränge" which are not found in the latter. *C. terebrans* differs from the six species described by Bovien (1926) in the host and in the possession of post-ovarian vitellaria. One other difference should be noted, all of the Caryophyllaeidae found thus far on the North American continent are found in members of the Catostomidae, see Essex and Hunter (1926), whereas those from Europe are typically found in the Cyprinidae. *C. terebrans* is readily distinguished

from all the species thus far described on this continent and is the only species recorded for the genus Caryophyllaeus.

GENUS MONOBOTHRIUM DIESING 1853.

Generic diagnosis: Caryophyllaeinae with scolex round to oval in cross section, bearing 6 shallow longitudinal grooves and terminal funnel-shaped introvert. Cirrus and utero-vaginal canal open together into a shallow, eversible, common genital atrium, widely separated by bulky annular pad (male genital papilla?). Ovary "H" shaped, entirely medullary. Uterine coils never anterior to cirrus sac, with maximum length one third that of testicular field, usually less. External seminal vesicle and terminal excretory bladder present. Post-ovarian vitellaria may or may not be present. Parasitic in digestive tract of Cyprinidae and Catostomidae. Development unknown.

Type species: *Monobothrium wageneri* [=*M. tuba* (v. Siebold 1853)] Nybelin 1922.

To include:

(1) *M. wageneri* Nybelin 1922
(2) *M. ingens* Hunter 1927

The author feels that in the light of the previous discussion this genus should be retained as valid. One of the criteria of usefulness is whether or not other new forms will fit into it. In 1927 the author published an account of a species which clearly and distinctly fell into the confines of this genus. The genus therefore has earned itself a permanent place in the classification of the Caryophyllaeidae.

MONOBOTHRIUM INGENS HUNTER 1927

[Figs. 8, 9, 29, 39, 79–83]

1927: *Monobothrium ingens* Hunter 1927:19

Specific diagnosis: With characters of genus. Adult parasites embedded in pits in mucosa of intestine. Length, 45 to 75 mm.; width, 0.9 to 1.2 mm. Neck distinct, 4 to 5 mm. long, 0.69 mm. maximum width. Longest longitudinal grooves on dorsal and ventral surfaces. Body broadens posteriorly, oval in cross section. Cuticula 5 to 6 μ thick; subcuticula 10 to 15 μ deep, bounded medianly by cortical layer of parenchyma which is 20 to 40 μ thick. Both inner and outer longitudinal muscle layers well developed and prominent. Testes 300 to 325, roughly ellipsoidal with maximum diameter of 0.192 to 0.298 mm. Cirrus sac lies at an angle of 45 degrees with horizontal, oval occupying about one half of medullary parenchyma; maximum diameter 0.35 mm.; circular muscles 12 to 36 μ thick. Female genital atrium opens into eversible cloaca, 0.19 mm. posterior to the male orifice. Vagina straight, not forming recep-

taculum seminis. Wings of ovary 0.8 to 1 mm. long; ovarian commissure 0.19 to 0.3 mm. in diameter. Vitellaria have maximum diameter of 0.18 mm. Post-ovarian vitellaria absent. Excretory system characterized by 10 pairs of main canals. Eggs 53 to 58 by 28 to 33μ.

Host: *Ictiobus cyprinella*, Lake Pepin, Minnesota. In intestine.

Type: Slides No. 29.40 in the collection of Dr. Henry B. Ward.

Paratype: Alcoholic specimens and slides in the author's collection Nos. 427, 428.

Host	Locality	Collector	Authority
Ictiobus cyprinella (Cuv. and Valenciennes)	Mississippi River, Lake Pepin, Minn.	G. W. Hunter, III and H. E. Essex	Hunter (the present paper)

Monobothrium ingens was parasitic in the intestine of *Ictiobus cyprinella* (large mouth buffalo). These worms were found with their scolices affixed in pits in the mucosa and submucosa. These pits were deep and also showed considerable proliferation of tissue, so that they protruded into the intestinal cavity. The size of the cysts was nearly uniform. The largest measured 17 by 14 mm. by 12 mm. in depth. Usually more than one parasite was found in a pit; the greatest number was 7.

The parasites themselves proved to be some of the largest of the Caryophyllaeinae, for when alive and in an extended condition they measured 65 to 75 mm.; this was not materially altered by fixing reagents. These parasites present a distinctly uniform exterior, as they were flattened dorsoventrally, with the exception of the neck and scolex which is more rounded than the other body regions. The cuticula is thick and gives a striated appearance to the surface of the worm.

The region of the scolex, although showing but little differentiation, is clearly marked off from the rest of the worm. It is about 2 mm. in length by 0.9 mm. in width and bears upon the dorsal and ventral surfaces two shallow and poorly defined loculi (Fig. 8). There are four others present, but these are more clearly visible in cross sections. Behind the scolex is a distinct neck, measuring approximately 0.69 mm. in width. This region is filled with a mass of excretory tubules which are visible in the toto mounts. The distance from the base of the scolex to the first of the vitellaria is variable due to the degree of contraction, but is between 4 and 5 mm. Posteriorly the body becomes broader reaching a maximum width of 0.9 to 1.2 mm. The body then tapers posteriorly until the region of the female reproductive system, just posterior to the cirrus sac,

is reached; here it has a maximum width of 1.11 mm. Unlike most of the Caryophyllaeinae the female reproductive system with the exception of the vitellaria is confined to the last twelfth of the body length.

The scolex of *M. ingens* places it clearly in the genus Monobothrium. It possesses a characteristic hexagonal scolex, each depression being a small loculus while at the anterior extremity is an eversible introvert (Figs. 8, 9). This fact may explain why the worms were uniformly found in pits in the musoca. The use of this organ is apparent if the living material is studied, for it was this portion of the parasite which was extruded for a considerable length and then retracted suddenly. The introvert may be turned in for a distance varying between 30 and 45 μ (Fig. 9).

In the study of sections no dark staining bodies appear for the first 50 μ. At this point, however, in a normally contracted specimen, the parenchymal cells as well as the tubes of the excretory system first appear. These tubes and tubules are confined to the region of the cortical parenchyma. This layer is bounded on the one hand by the outer longitudinal muscle bands and on the other by the large inner longitudinal muscles. About 0.3 mm. from the inner end of the introvert cross sections show cross muscle fibers dominating the region; these run at right angles to one another. The greater portion of them are inserted in the basement membrane of the scolex, although some of them may be seen attaching themselves to the fasciculi of the inner longitudinal muscle bands, while a few disappear into the parenchymal mass. The insertions, in the case of the dorso-ventral fibers, are in the region of the middle loculus; the lateral muscles are inserted on the median lateral surface of the parasite. In the center where these fibers cross at right angles are a number of deep staining parenchymal cells. These muscle fibers are found for a short distance only and are apparently highly specialized muscles. By contracting, they would cause a decrease in the breadth of the scolex thus aiding in the extension of the scolex. The neck region and posterior parts are incapable of much change, and it is known from observations on living material that the scolex is capable of considerable expansion. Thus it would seem that the contraction of these muscles at the base of the scolex would cause the elongation of this organ and the eversion of the introvert (Fig. 9).

The six loculi characteristic of the genus Monobothrium appear 0.11 mm. from the anterior extremity of the scolex and gradually disappear, except for the median ones on the dorsal and ventral surfaces, which run posteriorly for nearly one-third of the body length. These loculi are poorly defined and show little or no specialization. The only indication in this region is a slight thickening of the cuticula and cuticular muscles.

The cuticula of this Cestodarian parasite is composed of several layers.

The outermost portion is thin, being nearly 1 μ thick and stains readily with eosin. Under this lies the cuticula proper which has a thickness of 4 μ or more including the basement membrane. This latter structure measures nearly 1 μ across. These three layers, collectively known as the cuticula, are between 5 and 6 μ in width. There is little or no change in the thickness of these integumental layers in the different portions of the body, with the exception of the scolex where all three become slightly thicker. As is the case of all of the Caryophyllaeinae there are two layers of cuticular muscles which underlie the basement membrane. This muscle system is comprised of an outer layer of circular muscles, 1 μ in thickness, situated just beneath the basement membrane, followed by the longitudinal muscle layer of the cuticula which is slightly more prominent, being about 4 μ wide, and lying medianly to the circular muscles. The muscles just described are embedded in that portion called the subcuticula. This will be described in the paragraphs which follow.

The parenchyma of this parasite is divided into three portions, the outermost or subcuticula, the cortical and medullary parenchyma. The subcuticula extends 10 to 15 μ medianly from the basement membrane. In it are embodied the circular and longitudinal muscles of the cuticula, and a profusion of parenchymal cells. These cells form an irregular row lying between the longitudinal cuticular muscles on the one hand and the outer longitudinal muscle bands of the parenchymatous system on the other. These oval cells are characteristic, and stain deeply with hematoxylin; the nucleus and cytoplasmic bodies standing out with great clearness. Each cell is embedded in a mass of fibers which extend towards the basement membrane and roughly parallel one another. At the median border of the subcuticula is found the outer longitudinal muscle layer of the parenchymal system. These muscles are grouped 3 to 9 together in a fasciculus (Fig. 81). In the scolex the number of fasciculi are reduced and the fibers increase to 10 or 14 per fasciculus. The cortical layer of the parenchyma lies between the outer and inner longitudinal muscle bands. The parenchyma is less dense here and the cells are fewer in number. This is the region in which are found the paired longitudinal canals of the excretory system, the ascending canal being the more median.

The medullary parenchyma contains the reproductive systems, which in turn are surrounded by the inner longitudinal muscles. The fasciculi containing these muscle fibers are about 19 to 48 μ in width and lie 20 to 40 μ within the outer longitudinal muscles. In this layer the mass of parenchymal cells is greatly reduced due to the excessive specialization of the reproductive systems. Occasionally dorso-ventral and lateral muscle fibers are found. The former are more profuse, and extend across the medullary parenchyma, passing between the inner longitudinal muscles and frequently giving off fibers to them. Eventually these fibers reach

the subcuticula. Here they split and disappear into the base of the subcuticula where they are apparently inserted on the basement membrane (Fig. 81).

The musculature is similar to that of other closely related species of the Caryophyllaeinae and is composed of two distinct sets of muscles which are found in different parts of the body. The cuticular muscles have already been described in the portion dealing with the cuticula.

The parenchymatous muscle system is the most prominent one found in the body. It is composed of two sets of longitudinal muscle fibers and a set of sagittal (dorso-ventral) and frontal (transverse) muscle fibers. This system of muscles controls the action of the scolex to a large extent, although dealing primarily with its contraction. The longitudinal muscle system is composed of outer and inner longitudinal muscle layers, the former lies at the base of the subcuticula and separates it from the cortical parenchyma. In mature specimens these muscles appear to be in cavities in the parenchyma. This is the smaller of the longitudinal sets and each fasciculus is composed of only 6 to 9 individual fibers (Fig. 81). The muscles are 14 to 21 μ from the outer edge of the cuticula in the posterior portion of the body as compared with 24 to 28 μ in the middle part. This difference occurs, however, only in cases of the parasites whose uteri are distended by eggs. As the anterior portion of the body is reached the outer longitudinal muscles break up and disappear into the scolex. The inner longitudinal muscle mass is by far the most prominent one in this species. It extends from the anterior part of the scolex to the posterior extremity of the body. These as well as the outer longitudinal muscles are broken ventrally by the presence of the cirrus sac. The inner longitudinal muscles in the posterior tip are 96 to 108 μ from the outside. They help to keep the reproductive organs in position, as the testes and vitellaria tend to extend past these muscles and into the cortical parenchyma.

As the scolex is approached the subcuticular layer grows deeper and the longitudinal muscles of the cuticula are more distinct. Slightly more anteriad some of the inner fibers turn medianly and pass to the opposite side. On the ventral surface some turn and swing dorsally up and across to the dorsal side. This region of the base of the scolex is filled with many excretory tubules while in the medullary parenchyma a mass of unusual gland-like bodies appear, the exact function of which is uncertain. Branches from the inner longitudinal muscle mass, however, frequently penetrate to these cells. The inner muscles, contrary to the condition in some Caryophyllaeinae, especially *Glaridacris catostomi* Cooper (1920), do not divide into 8 large fasciculi in the neck, but retain the ring shaped formation. The bundles also increase somewhat in size in this region.

In cross and sagittal sections the dorso-ventral (sagittal) and lateral

(frontal) muscle fibers appear and may be traced. These are first found indistinctly in the lower portion of the scolex but from the neck posteriorly they increase in number and thickness. This is particularly noticeable in the case of the dorso-ventral fibers.

There are also certain specialized muscles which are found in various parts of the body. The first to be mentioned are the cross fibers found in the base of the scolex. These extend dorso-ventrally and laterally and aid in the elongation of the scolex. Their insertions lie in the basement membrane and the inner longitudinal muscles. The seminal vesicle is distinctly muscular, being surrounded with circular muscles. This condition pertains also in the ductus ejaculatorius, and in the cirrus sac to a less marked degree. The lower end of the uterus is also surrounded with circular muscles for a distance of 150 to 200 μ, and there is the sphincter muscle of the oöcapt between the ovarian reservoir of the commissure and the beginning of the oviduct. This completes the specialized musculature of *M. ingens*.

Little can be seen of the excretory system in toto mounts except a few longitudinal canals running throughout the body length. A close study of the anterior region, however, reveals the presence of a mass of tubules. In cross section this is very evident, the neck region and base of the scolex being filled with a mass of cross canals and smaller canaliculi. These tubules are difficult to trace, but it is apparent that they are confined to the region between the outer and inner longitudinal muscles. Ten pairs of main longitudinal canals in the neck region are so arranged that there are four ventral, four dorsal, and two lateral pairs of canals. Each pair is comprised of a large descending and a smaller ascending canal lying medianly to the descending one. These extend posteriorly and are connected by numerous cross passages. In all cases the smaller ones parallel the main descending canals. Finally in the region of the female reproductive system the small ascending canals are composed of smaller canaliculi originating in terminal excretory cells. These may be modified flame cells (Fig. 80). They appear at the ends of small tubules which are the beginnings of the ascending canals. The cell caps the tubule like a typical flame cell; it is 5 to 6 μ broad and does not appear very dissimilar from a typical parenchymal cell, thereby suggesting a common origin. The cells stain less deeply with hematoxylin than the parenchymal cells. Dark radiating strands are seen extending into the protoplasm of the cell. On the inner surface, projecting out into the tubule can be seen the cilia of the excretory cell. This flame cell is smaller than the "renal corpuscle" described by Cooper (1920) for *G. catostomi*.

The descending canals pass back into the posterior tip where they empty into a large excretory vesicle. This vesicle receives a number of tubes, the surface in cross section appearing serrated. The cavity is

about 166 by 75 μ in width and passes ventrally, growing smaller until a size of 60 by 25 μ is reached. The vesicle then tapers for 120 μ and passes to the outer ventral surface, through a canal 108 to 110 μ long by 36 μ wide. This canal is lined with cuticula and the entire vesicle is embedded in the subcuticular mass, which is characterized by a mass of parenchymal cells and the network of strands in which they lie.

There is one structure which appears in the neck and base of the scolex which will be described at this point, although the exact relation to the excretory system is doubtful. As the neck is reached and the excretory canals begin to branch profusely there appears an increase of the cells of the medullary parenchyma. These in turn give way anteriorly to a great number of large sac-like, irregularly-shaped bodies the granules of which take an eosin stain. Numerous branchings of the inner longitudinal muscular system can be traced through to these sac-like bodies. This condition continues on up into the mid portion of the scolex, where these bodies disappear. The function of these gland-like bodies is unknown. Two small ducts are evident which assume the position taken by the vitelline ducts in the posterior portion of the body. These ducts are situated laterally midway between the dorsal and ventral surfaces 15 to 25 μ from the lateral inner muscles of the longitudinal system. If they are connected with the excretory system they may function in the expansion of the scolex. Another possibility remains, these may be glands of the scolex, secreting fluids which aid the parasite in boring through the mucosa of the intestine of the host.

The nervous system is first seen in the scolex where the ganglia fuse. Two main branches can be traced posteriorly for a short distance, but they are soon lost.

The unusually large testes, averaging 0.228 mm. by 0.157 mm., number between 300 and 325 in an adult. The average number is between 312 and 318. This fact was determined by actual count of several specimens and by the estimation of the number of several more. A maximum of 0.298 mm. and a minimum of 0.192 mm. constitute the range of the main axis of the testes. The width shows a similar variation, for a maximum of 0.204 mm. and a minimum of 0.120 mm. were recorded. These figures are based upon the measurements of numerous testes, fifty of which are taken as typical examples. The longitudinal axis extends dorso-ventrally in most cases. It is possible, however, to occasionally find a form in which the main axis extends laterally. The easily recognized testes do not begin until approximately the middle of the body is reached. They are confined to the medullary parenchyma by the inner longitudinal muscles and the vitellaria. The latter are typically found scattered about the testes in a circle. The vitellaria are of such a large size, however, that they are readily confused with testicular tissue. Frequently

four of five testes, rarely six, are found in the same section and are usually grouped in pairs (Fig. 83). There are three rows of testes each of which may be broken into a dorsal and ventral portion, making three dorsal and three ventral. When the testes first begin they are not present in such great numbers, usually only two or three appearing together, and these will be both dorsal and ventral. Ocasionally a degenerating testis will be found. Two such were noted in one sexually mature specimen. Evidently the spermatozoa had been passed off and the remainder of the tissue underwent degeneration until little but the vacuity which had housed the testis remained. The testes extend posteriorly, interspersed with vitellaria until nearly opposite the cirrus sac. Those in the middle rows end first in order to make room for the convolutions of the vas deferens.

The vas deferens begins in the region of the first testis as a minute duct running an irregular course through the center of the body. As it proceeds posteriorly it gradually increases in size. Like the other Cestodaria the vasa efferentia are indistinguishable. As the testes increase in numbers the zig-zag course of the vas deferens is augmented by smaller tubes which connect with the outer rows of testes. These are perhaps more logically called *vasa deferentia secondaria*, for they are distinctly a part of the vas deferens system. As the vas deferens approaches the mid-testicular region the walls measure 5 to 7 μ and the diameter of the tube itself is 6 to 8 μ. This makes the vas deferens easy to trace as it has a total width of 16 to 25 μ. As it approaches the vicinity of the cirrus sac the testes and vitellaria gradually disappear from the center of the parenchyma, leaving the medullary parenchyma free from these structures in the shape of an inverted "V". This region is filled with the swollen convolutions of the vas deferens. It is filled with the spermatozoa and the wall is much thinner. The vas deferens, after making numerous convolutions, passes dorsally and medianly and enters a narrow muscular tube, the ductus ejaculatorius, which extends for 0.7 mm. before emptying into the seminal vesicle.

The seminal vesicle runs diagonally towards the ventral surface, the more dorsal portion being anterior. The vesicle, 0.28 mm. long and 0.19 mm. wide, contains a cavity 0.16 mm. by 0.04 mm. the latter surrounded by circular muscles. These muscles function in the ejaculation of the spermatozoa through the remainder of the ductus ejaculatorius and the cirrus. The former extends for 0.5 mm. from the seminal vesicle to the cirrus sac. It is thick walled with a diameter of 24 to 36 μ and is surrounded with circular muscles which aid in the ejaculation of the spermatozoa. The ductus ejaculatorius, therefore, has a total length of about 0.12 mm., 0.7 mm. before the seminal vesicle and 0.5 mm. after. This duct runs ventrally and enters the cirrus sac from the dorsal side (Fig.

29). It penetrates the end of the cirrus sac, instead of laterally as is the case in *Monobothrium wageneri.*

The cirrus sac is characteristic for the species and lies in a diagonal plane at an angle of 45 degrees with the vertical. It is embedded in the subcuticular mass which extends up into this region. The musculature is weak and the circular muscles extend about the cirrus; a few fibers run down into the tip of the papilla. In all the specimens examined this papilla was extended, although it might seem as though it were the papilla of an evertible cirrus. Such condition, however, seems doubtful since the musculature measuring barely 12 to 36 μ in width is so weak (Fig. 39). The breadth of the extruded portion, or papilla, is 0.293 mm. and the length approximately 0.233 mm. The diameter of the canal penetrating the papilla is 0.01 mm., while that of the cirrus sac proper is 0.03 mm. If the extra muscle fibers extending to the tip of the papilla are included the maximum width is 0.35 mm. The maximum length of the cirrus sac proper is 0.39 mm. and the "urethra" 0.36 mm. The thickness of the lining of this tube is 9 to 12 μ in the upper half and 4 to 7 μ in the lower portion of the cirrus sac. The lining appears to be a continuation of the cuticula.

The course of the spermatozoa is nearly the same as that described for other species of Monobothrium. The spermatozoa leave the testes, enter the *vasa deferentia secondaria* and thence pass to the vas deferens proper. Here they pass posteriorly and are stored in the lower part of the vas deferens. At the time of sexual activity the spermatozoa are drawn through the ductus ejaculatorius into the seminal vesicle by the action of the circular muscles surrounding it, out through the ductus ejaculatorius and into the cirrus sac and thence to the outside. In the case of self-fertilization the spermatozoa would pass into the genital cloaca, and into the vagina where they would be stored temporarily.

The female reproductive system is composed of vitellaria, ovary, ovarian reservoir, oöcapt, oviduct, oötype and shell gland, uterus and vagina. The vitellaria are found in the anterior portion of the body and lie entirely anterior to the cirrus sac. There are no post-ovarian vitellaria. These glands begin at the end of the neck region 4 to 5 mm. from the tip of the scolex. They extend posteriorly as far as the cirrus sac. Their position is quite characteristic of the Caryophyllaeinae in that a ring is formed about the testes. In this species the inner longitudinal muscles lie externally to the vitellarian circle. These glands are large and resemble the testes in size and shape. They range in size from 0.145 mm. to 0.180 mm. in length by 0.096 mm. to 0.144 mm. in width and are present in great numbers; there are between 720 and 740 in the sexually mature adult. This is based upon actual count of sections and is checked by the mathematical calculation of the number present. The vitelline

ducts are lateral and lie midway between the dorsal and ventral surfaces, just within the inner longitudinal muscles (Fig. 83). These ducts continue posteriorly and receive many smaller ones from the vitellaria themselves. The origin of such ducts may be seen in figure 79, where the tubule takes its origin from the middle of the vitelline follicle. Several follicular tubules unite to form the vitelline ducts. In the region of the ovarian commissure the vitelline ducts pass ventrally on the anterior side of the commissure and then turn medianly where they join and pass ventrally to emerge from beneath and join the vaginal-oviductal canal to form the uterus.

The H-shaped ovary measures 0.8 to 1.0 mm. in length; it is follicular and has a prominent ovarian commissure, the median portion of which functions as an ovarian reservoir. The commissure measures 0.49 mm. in length and has a diameter of 0.19 to 0.3 mm. The ovaries begin 0.48 mm. posterior to the female genital atrium and extend posteriorly until the body becomes pointed.

The oviduct is separated from the ovarian reservoir by the oöcapt. In it is a distinct layer of circular sphincter muscles. These measure 0.048 mm. in cross section. These sphincter muscles control the release of the ova. The oviduct extends ventrally until it meets the vagina and later the vitelline duct. The vagina runs anteriorly and dorsal to the oviduct and ventral to the main portion of the uterus. Just before joining the oviduct the vagina is surrounded by circular muscles 2 to 3 μ thick under which is a thin non-cellular layer 2.1 μ thick and above lie the muscle cells 15.9 μ wide. The width of the entire cavity is 10.6 μ. There is no distinct receptaculum seminis. As the more anterior portion of the vagina is reached the lining measured 0.9 μ and the circular muscles 5.3 μ. This empties after a relatively straight course into the cloaca from the side, and thence passes to the exterior.

The combined oviduct and vagina meets the common vitelline duct within the confines of the oötype. Here the tube is very narrow and the oötype is made up of numerous loose, glandular cells. Ducts originating from the oötype empty into the vitelline ducts before they reach the vagina. These ducts arise from single cells, which appear in the oötype as large glandular cells. These cells may secrete something which aids in the formation of the shell of the ovum. It is probable that these cells and their secretions must have some function which is connected with that of the formation of the shells for the ova, since the vitelline material and the fertilized ova all appear at this spot.

The oötype soon permits the convoluted uterus to broaden slightly as it passes posteriorly. After reaching the posterior limits of the oötype the uterus proceeds anteriorly and passes from the oötype becoming thin walled. This duct turns back upon itself and zig-zags back and forth

behind the arms of the ovary, passing from the right to the left sides in three convolutions. The uterus then runs anteriorly, the main limb passing dorsally to the ovary. Anterior to the ovarian commissure it becomes thick-walled and lined with pear shaped cells, characteristic of the uterine glands. The uterus makes several loops and convolutions, passing from one side to the other before it empties into the cloaca. Ninety to 100 μ before the emptying of the uterus into the vagina, the thick walled cells become less and circular muscle bands 3 to 5 μ thick take their place. The functions of these muscles are two fold, in the first place they serve to keep the eggs from being discharged until the time is propitious for their release, and secondly they serve to keep the distal end of the uterus closed at the time the spermatozoa are passed into the vagina (Fig. 39).

The female cloaca is formed by the union of the vagina and uterus. The latter enters from the right side into the vagina which runs ventrally from a more dorsal position. The opening of the uterus is 0.12 mm. wide at its point of entrance into the cloaca. The vagina leaves from a dorsal and posterior position. It is surrounded throughout its entirety by circular muscles. The cloaca passes ventrally for 0.19 mm. where it opens into a fairly large atrium situated posteriorly to the papilla of the cirrus. It measures 0.24 mm. by 0.96 mm. at its widest place. The minimum width is 0.025 mm (Fig. 39). The distance from the middle of the papilla to the center of the atrium is 0.19 mm.

The eggs of this species are fairly large, ovoid and average 57.2 by 30.4 μ Measurements were made of the eggs in sections many of which were at different developmental stages. The eggs range from 53 to 58 μ in length by 28 to 33 μ in width.

According to the revision of the genus Monobothrium the form which has just been described clearly falls into this genus. The scolex is nearly structureless, being rounded anteriorly and possessing 6 shallow longitudinal grooves and a terminal introvert. The ovary is "H" shaped and compact while the cirrus and utero-vaginal atrium open together into a shallow eversible cloaca; the male system is separated from the female by an annular pad (male genital papilla?).

There has only been a single species described as belonging to this genus, *Monobothrium wageneri* (=*M. tuba*). The new species, *M. ingens*, Hunter (1927) has a maximum length of 45 to 50 mm. which is greater than the 22 to 24 mm. recorded by Nybelin (1922:118) and the maximum length of 33 mm. noted by Sonsino (1891) for *M. wageneri*. In *M. ingens* the cuticular, outer and inner longitudinal muscles are present clearly dividing the tissue outside the inner longitudinal muscles into cortical and subcuticular layers. The testes have a maximum diameter of 0.19 to 0.29 mm. and number 300 to 325 in comparison with *M. wageneri* which has testes measuring 0.16 to 0.18 mm. The cirrus sac in the latter measures 0.40 to

0.45 mm. long by 0.28 mm. broad which is in marked contrast to a maximum length of 1.48 mm. and a breadth of 1.3 mm. recorded for *M. ingens*. In all of the specimens examined the cirrus sac was found to lie at an angle of nearly 45 degrees with the vertical. The genital atrium is typical of the genus and both possess the characteristic annular pad, or male papilla (?). The vagina in both cases is relatively straight, neither one forming a distinct receptaculum seminis. The oöcapt arises on the mid line and not laterally as in *M. wageneri*. The vitellaria in the latter are small, measuring ing 0.07 to 0.1 mm. in comparison with 0.14 to 0.18 mm. for the former. The oötype and shell gland has a diameter of 0.5 mm. in *M. wageneri* and of 0.4 to 0.75 mm. in *M. ingens*. The eggs of the former are much larger and measure 75 to 78 μ in length and 48 μ in width compared with a length and breadth of 53 to 58 μ and 28 to 33 μ respectively in *M. ingens*.

GENUS GLARIDACRIS COOPER 1920

Generic diagnosis: Caryophyllaeinae with three pairs of loculi or bothria on well defined scolex, which may or may not form a definite terminal disc. Cirrus opens on ventral surface or into a shallow, non-eversible genital atrium. Ovary "H" shaped and entirely medullary. Coils of uterus never extend anteriorly to cirrus sac, and reach a maximum longitudinal length of one third that of testicular field, usually less. Terminal excretory bladder and external seminal vesicle present. Post-ovarian vitellaria present. Parasitic in digestive tract of the Catostomidae.

Type species: *Glaridacris catostomi* Cooper 1920.

To include:

(1) *G. catostomi* Cooper 1920.
(2) *G. hexacotyle* (Linton 1897).
(3) *G. laruei* (Lamont 1921).
(4) *G. confusus* Hunter 1929.

In earlier papers of Woodland (1923, 1926) this genus is deleted and the type species was placed provisionally in the genus Caryophyllaeus. Since that date it has been shown that the genus is really valid and that two other species also fall into this group, *G. hexacotyle* and *G. laruei*. The addition of a fairly common new species to this genus, *G. confusus*, increases the total of valid species to four and erases the possibility of this genus being deleted. It is significant and interesting to note that this genus is apparently confined to this continent as there have been no other records reported even though a number of new species have been described.

GLARIDACRIS CATOSTOMI COOPER 1920

[Figs. 2, 25, 44, 45]

1920: *Glaridacris catostomi*	Cooper	1920: 5–24
1923: *Caryophyllaeus catostomi*	Woodland	1923: 435–472
1924: *Glaridacris catostomi*	Johnston	1924: 347

1925: *Caryophyllaeus catostomi*	Moghe	1925: 232–235
1926: *Caryophyllaeus catostomi*	Woodland	1926: 56
1927: *Glaridacris catostomi*	Hunter	1927: 19

Specific diagnosis: With the characters of the genus. Adults up to 25 mm. in length with a maximum breadth of 1 mm.; may be buried in pits in mucosa, altho this condition is more typical of the larvae. Scolex short, broad and chisel-shaped, length varying between 0.3 and 0.45 mm. Neck distinct, slightly narrower than body which is flattened dorso-ventrally and bears a conspicuous genital atrium. Cuticula 7 to 11 μ thick, subcuticula 12 to 16 μ in depth; this in turn is bounded internally by outer longitudinal muscles. These muscles separate it from the cortical parenchyma which has a depth of 70 to 84 μ. Both inner and outer longitudinal muscles are present and prominent. The testes number between 405 and 420 and are irregularly ellipsoidal with a maximum diameter of 0.12 to 0.19 mm. Cirrus sac ovoid to spherical, occupies the entire medullary parenchyma, possessing a maximum diameter of 0.4 to 0.6 mm. Common genital atrium conspicuous, 0.4 to 0.5 mm. long, 0.7 to 0.16 mm.; female reproductive system opens 0.13 mm. posterior to that of the male. Vagina median, ventral, convoluted and forms an indistinct receptaculum seminis. Wings of the ovary 0.65 to 0.9 mm. long; prominent ovarian commissure 0.4 mm. in diameter. Vitellaria with maximum diameter of 0.2 mm.; expanded common vitelline duct functions as vitelline reservoir. The excretory system has 8 to 10 pairs of canals with terminal excretory bladder measuring 0.25 by 0.05 mm. Eggs operculate, 54 to 66 by 38 to 48 μ.

Host: *Catostomus commersonii*, Douglas Lake, Mich.; Burntside Lake, Minn.; Lake Erie, Silver Creek, New York.

Type: Cooper's original slides in the collection of Dr. Henry B. Ward. No. 25. 137.

Host	Locality	Collector	Authority
Catostomus commersonii (Lacépède)	Douglas Lake, Mich.	A. R. Cooper	Cooper 1920: 5–24 Hunter (the present paper)
Catostomus commersonii (Lacépède)	Burntside Lake, Minn.	H. E. Essex	Hunter (the present paper)
Catostomus commersonii (Lacépède)	Lake Erie, Silver Creek, N. Y.	G. W. Hunter, III	Hunter (the present paper)

Glaridacris catostomi was originally described by Cooper (1920) and designated as a new genus and species. At that time the author thought that this form was the first to be described from this continent, and was in ignorance of the two forms noted by Linton in 1893 and 1897. Some years after publishing this description all of the slides and material were turned over to Professor Henry B. Ward, who was kind enough to loan the specimens to me for comparisons with other material. Since the original work was found to be at fault in several instances it seemed advisable to publish the corrected description ensemble.

The material was obtained at the Douglas Lake Biological Station of the University of Michigan, where a total of 36 specimens of the host, *Catostomus commersonii* (Lacépède) was examined. The younger fish ranged in size from 90 to 115 mm. and were obtained by seining them out of the Maple River; these were uninfected with Cestodaria. The adults, however, were taken in fyke nets from the lake and 11 of the 26 were parasitized.

Most of the larvae and all of the adults were found free in the stomach or the intestine, but as Cooper (1920: 6) says, many of the larvae were found,

> attached to the bottoms of deep pits in the mucosa of the pyloric region of the stomach. These pits were not mere depressions of the wall of the stomach but actual cavities, ... bordered by a pronounced annular thickening of the mucous membrane and as much as 2 mm. in diameter. Larvae ranging in size from almost the smallest met with to those near the adult stage in development were tightly crowded into these pits and at the same time strongly contracted longitudinally.

This description is typical of the larvae of this species.

Inasmuch as the musculature of this species is well developed the contraction of the individuals varied considerably but the length of the adults ranged from 5 up to 25 mm. and from 0.4 to 1 mm. in maximum breadth. In the larvae the scolex shows little or no differentiation and the body tapers behind to a blunt tip at the posterior extremity. Often the body appeared wrinkled due to the contraction. In adults the scolex presents several different shapes, the typical shape appearing in figure 2. The neck lies behind the scolex and, as is typical for the members of this genus, is the narrowest portion of the body. This region varies from 1.5 to 2.5 mm. in length. The body broadens posteriorly and the posterior extremity is slightly indented at the point where the excretory vessels open to the outside.

The scolex of the adults is characterized by the presence of three loculi on the dorsal and ventral surfaces, and these are accentuated by the muscle bands which extend towards the distal end forming a broad tip, which is somewhat chisel-shaped. It differs from *G. hexacotyle* in not having the loculi unite to form a single, pointed conical apex. The length of the scolex varies between 0.30 and 0.45 mm.; the width between 0.45 and 1.10. mm; and the depth (posteriorly) between 0.50 and 0.75 mm. In the base of the

scolex are found the eight large fasciculi of the inner longitudinal muscles. Posterior to this lies a large mass of cells characterized by large nuclei; the cytoplasm contains numerous granules having an unusual affinity for counterstain. These are probably glandular for they send out long processes in a diagonal direction to the cuticula.

The cuticula varies in thickness from 7 to 11 μ and is bounded medianly by the relatively heavy basement membrane extending one-sixth the thickness of the entire layer. The remainder of the cuticula has something of the appearance of a reticulum described by Cooper (1920:8-9) as follows:

This reticulum is in reality a meshwork of fine canaliculi which freely pierce both limiting membranes, thus giving them the appearance in tangential sections of fine sieves. Nowhere is the cuticula modified to form spinelets nor distinct cirri, although over the scolex it is considerably folded and irregular, the outer membrane being all but absent, especially within the suckers.

The subcuticula is composed of large flask shaped cells, having rather large nuclei. The entire layer is 90 to 100 μ in thickness. The spherical to ovoid nuclei are crowded together, measure 16 to 18 μ in greatest diameter. The nucleoli are spherical. This area is considered as one by Cooper, but is divided into two parts. The outer or subcuticula extends 15 to 30 μ from the cuticula and is separated from the more median cortical parenchyma by the band of outer longitudinal muscles. This division is rather arbitrary and does not occur in all of the species studied, but when it does occur it should be noted and used. The main longitudinal canals of the excretory system are confined to the cortical parenchyma. The cells of the parenchyma are distinctly different from those of the subcuticula, the distinction being largely one of contrast with the subcuticula cells. The former take the stain deeply while the latter are marked by their clear, non-granular cytoplasm.

The musculature is composed of two sets, the cuticular and the parenchymatous. This parasite has both sets well developed. The circular muscles of the cuticula are slightly over 1 μ in thickness and lie close beneath the basement membrane. Inside this layer are found those fibers belonging to the longitudinal cuticular system. There are 2 or 3 and sometimes more, in a fasciculus, and Cooper (1920) reports that sometimes these muscles intermingle with those of the outer longitudinal system. The parenchymatous muscles are very prominent. The outer longitudinal muscles are arranged in small bundles, each containing upwards of fifteen fibers in a bundle. The size of these bundles is more uniform than the inner longitudinal groups and they lie 15 to 30 μ from the outside. Posteriorly these fibers and those of the longitudinal cuticular system intermingle as they become embedded in the wall of the excretory bladder. The muscles of the inner longitudinal system are by far the most prominent; they are found 60 to 100 μ from the outside and there are up to 25 fibers in the fasciculi.

In the neck these are collected together so that eight large bundles are formed (cf. Fig. 61). Cooper (1920:11) describes these as follows:

. . . . the eight large bundles of inner longitudinal muscles, mentioned above, are arranged so that four form two sagittal pairs situated towards the lateral faces, while the other four, somewhat larger ones form two other sagittal pairs, each about half way between the nerve trunk and the median line. These are distributed in a radiating manner to the corresponding portions of the tip of the scolex, the median pairs going to the ridges between the loculi and the neighboring pairs of the latter. On the whole their attachment is similar to that of the main longitudinal group in *C. tuba* and *C. laticeps*, as described respectively by Monticelli (1892) and Will. The outer longitudinal muscles are more numerous on the lateral surfaces of the scolex than opposite the suckers, to the cuticula of which they are easily traced. The loculi are also provided with a few scattered radiating fibers, lying in both the longitudinal and transverse directions, and comparable to those used in the Pseudophyllidea for the enlargement of the bothria. They are, however, of much less functional importance in that connection than the sagittal and transverse fibers, which are somewhat larger and more numerous than in the middle of the worm. In fine, the musculature of the scolex is poorly developed as compared with that of *Bothriocephalus*, s. str., for example, which fact is shown in the great diversity of shapes of the organ in preserved material.

The nervous system was worked out by Cooper in his original description and as no errors were found the description is quoted verbatim.

The nervous system consists of a pair of ill-defined longitudinal trunks and two equally indistinct and diffuse terminal ganglia situated in the scolex, into which they pass. The main strands can be followed more or less easily in material not especially treated to demonstrate them only in the neck region. There, ... they are situated symmetrically in the median frontal plane within the trapezium formed by the two pairs of main longitudinal muscle bundles, much closer, however, to the lateral pair than to the more median pair. They supply these muscles with large branches. Whereas in the neck they are fairly uniform in diameter—which varies from 18 to 30 μ—behind the most anterior vitelline follicles they become quite irregular in transection, all but disappearing in places. In the middle of the worm and posteriorly they seem to break up into a diffuse plexus lying just within the subcuticular cells, that is, among the numerous bundles of the inner longitudinal muscles. No collateral strands such as the eight described by Will for *C. laticeps* were seen in this form.

In the base of the scolex these chief nerve strands expand considerably in the dorso-ventral direction and become united by a few transverse fibrils. Farther towards the tip, however, each of these enlargements divides into two parts sagittally, and each of the latter unites with its fellow of the opposite side by a loose strand of transverse fibrils, so that two anteriorly directed loops are thus formed. On the whole the nervous system is comparatively poorly developed, since not only the chief strands but also their connections in the scolex are composed of very fine, indistinct and loosely arranged fibrils.

The excretory system consists of ascending and descending canals in pairs; and therefore do not differ from the typical systems. Anteriorly there are eight main channels, located three on each surface and one at each lateral margin. As the neck is reached the tubes break up into numerous plexuses. These canals and canaliculi invade all parts of the subcuticula and the cortical parenchyma. About 1 to 1.3 mm. from the tip of the scolex two branches leave the plexus above and below the nerve cord and unite "on the medial side of the latter to form one vessel. In these positions

the two vessels thus formed pursue spiral courses forward and apparently unite close behind the nerve commissures mentioned above." (Cooper.) The main descending canals of this system find their way to the unusually large excretory vesicle. It measures 0.25 mm. in length by 0.05 mm. in width, and appears as an invagination of the hinder portion of the parasite, for the wall is composed of a lining of cuticula identical with that found on other surfaces. A few circular muscles were detected about this vesicle; the main muscles of both longitudinal systems also give off fibers which are embedded in the walls of the vesicle which empties on the median ventral surface at the posterior tip of the body. True flame cells were not present. In their place are the renal corpuscles which were first described by Cooper (1920:13-14). Each cell is composed of a distinct nucleus and nucleolus, with a cytoplasm which is highly vacuolated. The bulk of the cytoplasm lies about the nucleus with only strands radiating out to the wall of the cell, which are continuous with the wall of the canaliculus leading to the ascending canal. The probable mechanism by which these cells function is discussed on page 13 (Cooper 1920).

The male reproductive system is of interest in several respects. The testes are very numerous and rather large. They are completely surrounded by the vitellaria and are irregularly ellipsoidal in shape numbering 405 to 420 in the normal adult. This number was checked by actual count and also by an estimation of the number present. The method is described in detail on page 11. In the more anterior portion of the body the testes are smaller than they are posteriorly; they are arranged in two rows one of which is dorsal and the other ventral. There are two or three testes in each row (Fig. 45). Various stages of spermatogenesis were visible in the different testes and also it was possible to find some of the spermatozoa in the more distal portions of the vas deferens. This is contrary to Cooper's findings but they are clearly present in one of the adults which were sectioned by the author. At the same time eggs were present in the uterus. In normal conditions the spermatozoa mature first.

The vas deferens is formed by the union of various branches of the vas deferentia secondaria which extend from the testes to the vas deferens. Each tube will tap three or sometimes four testes and bring these products to the vas deferens. As the cirrus sac is approached the vas deferens forms a loose, triangular mass of coils which measures about 0.32 mm. in length, 0.36 mm. in depth, and 0.28 mm. in width. A short distance before passing into the cirrus sac the vas deferens becomes narrower and enters the muscular ductus ejaculatorius. This almost immediately expands to form the seminal vesicle which structure is about 0.30 mm. in length and has a diameter varying between 0.065 and 0.090 mm. The wall of the duct consists of an epithelium syncitial in nature, in which are embedded widely separated nuclei. About this layer lies the muscles which are composed principally of

circular muscles and a few oblique fibers scattered among them (Fig. 25).

The vas deferens enters the cirrus sac from the anterior dorsal surface. At the point of entrance it measures about 30 μ, this soon expands in the dorsal third of the cirrus sac to form a secondary, but probably temporary, seminal vesicle with a maximum diameter of 60 μ. The size soon diminishes and the cirrus proper is reached. The cirrus occupies the lower half of the cirrus sac and has a diameter of 60 to 65 μ. The lining of cirrus is smooth cuticula which is continuous with that of the ventral surface of the worm, and above this may be found the circular muscles in slightly greater numbers than about the walls of the ductus ejaculatorius. The cirrus sac occupies the whole of the medulla of this region dorso-ventrally and almost all of it laterally. It is ellipsoidal in shape and its maximum diameter varies between 0.4 and 0.6 mm. The wall is composed of muscular fibers surrounding the sac and extending in all directions. A few of the dorso-ventral fibers pass from the top of the sac into the dorsal body wall and some from the lateral position of the sac pass to the ventral body wall. Within this layer are found numerous retractile muscle fibers which are attached to various parts of the cirrus; their exact insertion could not be ascertained with accuracy from the material available. The myoblastic nuclei of the retractile muscles as well as a small amount of parenchymal tissue is also present.

The female genital atrium lies 0.5 to 0.13 mm. posterior to that of the male and opens into the common atrium (Fig. 25). This common atrium is about 0.45 to 0.55 mm. in largest diameter and has a depth of 0.7 to 0.16 mm. Because of its relatively great length it does not appear to be particularly deep. The female genital atrium lies posterior to the male, and is much more conspicuous, having a diameter of 0.12 to .168 mm. at the point of entrance into the common atrium and a maximum depth of 0.2 to 0.3 mm. The opening is crescentric and narrows as it progresses medianly to 0.4 to 0.7 mm. part of the way up. The cortical parenchyma surrounds the female genital atrium to a marked degree so that the outer longitudinal muscles are forced medianly at this point. The uterus enters the female atrium, 0.2 to 0.3 mm. from the surface in the median portion of the body laterally and from the left. The vagina empties slightly nearer the surface than the uterus and on the opposite side (Fig. 44).

The ovary is irregularly lobate and is situated about half way between the genital atrium and the posterior body tip. (See Fig. 25.) It is from 0.65 to 0.9 mm. in length and with the prominent ovarian commissure forms the "H" so characteristic of this group. In cross section the ovary occupies nearly the entire medullary field, except for the uterus, which lies dorsal and median to it. The vagina lies beneath and the vitelline ducts parallel each ovarian wing which has a depth of 0.4 to 0.45 mm. and a wing width of 0.2 to 0.25 mm. The ovarian commissure leaves about the center of the

wing of the ovary and extends medianly. It is spherical in cross section and has a maximum diameter of 0.4 mm. The median portion of this commissure functions as an ovarian reservoir and contains ova ranging in size from 13 to 18 μ in length by 10 to 15 μ in width. The majority of them are nearly spherical and measure in the neighborhood of 15 μ.

The vitellaria are found in two separate and distinct fields, one extending from the neck to the cirrus sac and the second confined to that portion of the body between the posterior coils of the uterus and the posterior extremity of the body. In the anterior portion of the body they form a distinct layer about the testes and vary in number from 8 to 15 in cross sections (Fig. 45). These glands become slightly larger posteriorly and have a maximum diameter of 0.2 mm. The process of the formation of the yolk cells is clearly described by Cooper (1920:18-19) as follows:

> The cytoplasm of the small peripheral primordial cells from which they develop is very compact, and consequently stains deeply as does the nucleus. Numerous vacuoles appear in it and quickly enlarge, so that in the intermediate stages the nucleus appears to be suspended in the center of the cells by protoplasmic strands radiating from it to the cell membrane . . . . . These strands become modified into numerous, spherical deutoplasmic granules, migrate outward and eventually come to lie just inside the cell-membrane. In the proximal part of the uterus, where from four to six vitelline cells are seen to be associated with each fertilized ovum in the formation of the egg, the nucleus enlarges still more and becomes more transparent, while the cell-wall gradually breaks down, thus liberating the vitelline granules. The enlarged nuclei remain intact, however, during the passage of the egg through almost the whole length of the uterus.

The vitelline ducts are four in number, but are reduced to two as the cirrus sac is approached. These two ducts take a median position on each side of the vagina and pass posteriorly. They measure 7 to 50 μ in diameter depending upon the presence or absence of the vitelline follicles. As the ovarian commissure is approached the two vitelline ducts join to form a common vitelline reservoir lying dorsal to the commissure. The vagina lies above, and dorsal to it the uterus. The reservoir ranges in size between 30 and 100 μ. Upon reaching the ovarian commissure the common vitelline duct is joined by two small ones from the post-ovarian vitellaria. Immediately the common vitelline ducts divide into an upper and lower reservoir, one end of which is blind. The single vitelline duct passes over the dorsal surface of the posterior edge of the ovarian commissure and becomes very narrow, the diameter dropping from 20 μ to almost nothing. At this point the oötype is penetrated and as the duct passes towards the center of this structure several minute ducts were found to empty into it from various parts of the oötype. Soon this canal continues dorsally and to the left and empties into the combined vaginal-oviducal canal, or fertilization chamber. The course of the vitellarian duct within the oötype is outlined by the myoblastic nuclei which are found 6 to 8 μ from the canal itself, and surround the few thin muscles about the canal.

The vagina passes posteriorly from the female genital atrium just beneath the coils of the uterus. The diameter near the point of origin is between 50 and 55 μ; this is reduced to 30 μ or less as the canal passes posteriorly. The vagina is lined with a layer of cuticula about 5 μ in thickness which in turn is surrounded by numerous circular muscles whose myoblastic nuclei form a distinct layer about 10 μ from the fibers. The canal is convoluted and as it passes posteriorly is pushed dorsally to the center as the ventral portion of the ovary becomes filled with the ova to form the ovarian reservoir. As the vitelline ducts expand the duct is pushed further dorsally; soon the vagina, measuring about 25 to 35 μ in diameter, passes to the right and the vitelline duct comes up and fills the left median portion of the medullary parenchyma. An indistinct receptaculum seminis is formed and this soon gives way to the narrow vagina, now 7 to 12 μ in diameter, which dips ventrally over the posterior edge of the ovarian commissure to become enveloped in the oötype (Fig. 44).

The oöcapt arises from the median posterior surface of the ovarian commissure. It measures 29 to 32 μ in cross section and the canal is surrounded by circular muscles 10 μ in thickness forming the sphincter which controls the release of the ova from the ovarian reservoir. The oviduct is extremely long, about 0.2 mm. in length and has a diameter of 21 to 23 μ which is reduced to 9 or 10 μ before joining the vagina which passes up from a more ventral position to form the fertilization chamber. This oviducal-vaginal canal passes to the right, is joined by the single vitelline duct, dips ventrally, just keeping within the bounds of the oötype and curves back on itself to leave the oötype near its posterior extremity. The oötype is rather prominent and has a maximum diameter varying between 0.38 and 0.42 mm.

The uterus leaves the oötype posteriorly and passes through several convolutions, the walls being lined with syncitial epithelium. It soon enlarges and becomes filled with eggs. The size increases and its wall becomes thinner until it turns anteriorly to pass dorsally over the ovarian commissure. As the posterior tip of the ovary is passed the uterus becomes surrounded by a mass of unicellular and club shaped glands. The uterus is surrounded with only a few scattered muscles until the region of the female atrium is reached when the glands give way to the myoblastic nuclei which surround the muscles of this region. Inasmuch as Cooper examined fresh eggs from this species his description is repeated verbatim.

> The mature fresh eggs, when examined in normal saline solution, were found to be ovoid in shape and from 54 to 66 μ in length by 38 to 48 μ in width. The shell is from 2 to 3 μ in thickness, and is provided at its larger end with a small button-like boss and at its smaller end with an operculum from 12 to 16 μ in diameter.

G. catostomi because of the position of its sexual apertures and ovary,

the annular arrangement of the vitellaria about the testes which are surrounded by the inner longitudinal muscles, falls into the Caryophyllaeinae. The genus Caryophyllaeus is characterized by a broadened or curled anterior extremity which is not specialized into a scolex, and the absence of an external seminal vesicle. In this last respect it differs from *G. catostomi.* Other differences of the scolex and genital atrium keeps this species from the genus Monobothrium, while it differs from Caryophyllaeides in the lack of specialization of the scolex, type of genital atrium and the presence of the uterine coils anterior to the cirrus sac. In these three characters it also differs from the genus Biacetabulum, and it is separated from the genus Hypocaryophyllaeus by the presence of the uterine coils anterior to the cirrus sac. Clearly then this species does not fall into Caryophyllaeus, Monobothrium, Caryophyllaeides, Biacetabulum or Hypocaryophyllaeus. However, it does fall into the one remaining group, Glaridacris, for it possesses three pairs of loculi on a well defined scolex, the cirrus opens into a shallow genital atrium while the ovary is "H" shaped and medullary, the coils of the uterus are not anterior to the cirrus sac, there is an external seminal vesicle, and this form is parasitic in the intestines and stomach of the Catostomidae. It differs from the other forms thus far described from this continent in several respects. In the first place *G. catostomi* is clearly separated from the other two species described by the type of scolex, for *G. laruei* possesses the "Π" type, and *G. hexacotyle* has six weak loculi, forming a conical apex which distinguishes it from *G. catostomi.* The cuticula of this latter species is 7 to 11 μ in thickness and is thicker than the 2 to 3 and 3 to 5 μ cuticula measurements of *G. laruei* and *G. hexacotyle.* Again the number of testes facilitates the determination of the species. *G. catostomi* has 405 to 420 while *G. hexacotyle* and *G. laruei* have respectively 175 to 200 and 60 to 85. The cirrus sac of *G. catostomi* occupies the entire medullary parenchyma, laterally as well as dorso-ventrally thus serving as an excellent means of differentiation. The circular muscles about the cirrus sac are also nearly twice as thick as those found in the other species under consideration. Furthermore, this species possesses a very prominent genital atrium which is 0.4 to 0.5 mm. in greatest diameter and 0.07 to 0.15 mm. in depth. Such an atrium is not characteristic of the other two species belonging to this genus. The female atrium, opening into the common cavity is 0.13 mm. posterior to that of the male in Cooper's form while it is 12 to 19 μ and 20 to 26 μ behind that of the male in *G. laruei* and *G. hexacotyle.* The vitellaria surround the testes with 8 to 15 in view in transsection and the expanded common vitelline duct serves as a reservoir. In this respect it differs from *G. hexacotyle* in which the expanded ducts function as vitelline reservoirs and the anterior group of vitellaria are confined to two lateral fields within the inner longitudinal muscles. *G. catostomi* differs from *G. laruei* and *G. hexacotyle* in the absence of a distinct receptaculum seminis.

The eggs of *G. catostomi* are much larger, ranging between 54 to 55 μ by 38 to 48 μ, while those of *G. hexacotyle* and *G. laruei* have a maximum length and breadth of 42 $\times 30$ μ. The excretory bladder of this species is larger than that of *G. hexacotyle* and *G. laruei*, measuring 0.25 by 0.05 mm. compared with 0.045 to 0.048 by 0.024 mm. for the latter two forms.

Cooper (1920) in his original paper describes two different types of scolices for his new species *Glaridacris catostomi*. To quote:

> In immature individuals the scolex, when nót strongly contracted, has somewhat the form of a truncated rectangular pyramid with the longer diameter in the transverse direction . . . . the edges of the base and the apex protrude markedly, in the latter case forming a terminal disc comparable to that of many of the bothriocephalid cestodes. The dorsal and ventral surfaces of the organs are each divided by two ridges converging towards the apex into three sucking grooves or loculi, of which the middle is best developed and most efficacious during life. It is also the last to become smoothed out with the strong contraction of the whole scolex. The lateral loculi are, furthermore, not in the same plane with the medial one but inclined towards the corresponding ones of the opposite surface so that the edges of the scolex, especially just behind the terminal disc, are often not much thicker than the ridges between the loculi . . . . . In adults, on the other hand, the edges of the terminal disc are usually found in preserved material to be contracted to the point of obliteration, so that the whole organ is shaped more like a wedge or chisel with oftentimes rather thick margins. As a matter of fact the scolex of this form assumes a greater variety of shapes than that of any other tapeworm I have yet examined, in which respect it is comparable to the leaf-like anterior end of Caryophyllaeus.

Cooper's original vials and slides were placed at my disposal through the kindness of Professor Henry B. Ward. Also some vials of Cestodaria taken from *C. commersonii* from Douglas Lake, Michigan were loaned by Dr. George R. LaRue. Upon examination of this material (75 or 80 individuals collected over a period of years) it is apparent that at least *two* species of Cestodaria are present. Under binoculars it is a relatively simple matter to distinguish the larvae of *G. catostomi*. They are thicker, with a greater breadth anteriorly and taper posteriorly to a blunt point. The scolex is structureless and shows little or no differentiation at this stage. At the margin of the last quarter of the body, however, lies the genital atrium, conspicuous even in specimens only 1.9 to 3.3 mm. long. At the same time members of the species *G. laruei* can also be detected with ease. These forms are longer and narrower and possess the type of scolex characterized as the "Π" type because of its resemblance to this Greek letter. These larvae may be further distinguished by the absence of the conspicuous genital atrium which was characteristic of the 25 larvae of *G. catostomi* which were examined. Sectioned material shows other differences between these two species. First the cuticula is vastly different, and this character alone would serve to differentiate them, for on *G. laruei* it never exceeds 2 to 3.5 μ in thickness and is perfectly smooth. Upon the other hand the cuticula of *G. catostomi* is pigmented, takes a deep blue stain and measures about 25 μ in depth, except for the scolex where it is reduced to about

4 or 5 μ in thickness. This layer besides being unusually thick and pigmented possesses rather characteristic depressions extending to within 4 to 6 μ of the basement membrane. This gives a distinctly serrated appearance in the sectioned material. Another means of distinguishing these larvae from *G. laruei* lies in the fact that the common genital atrium or cloaca is prominent in specimens of less than 2 mm. and even at this stage has a depth of 0.8 to 0.14 mm. The female reproductive organs open in the posterior end of this cavity and the male in the anterior. These figures coincide with the depth of 0.7 to 0.15 mm. noted for the adults. It is evident therefore that Cooper in his original description confused these two forms and that the scolex which he describes for the larval stage is in reality that of *G. laruei*.

GLARIDACRIS HEXACOTYLE (LINTON 1897)

[Figs. 3, 19–21, 41, 42, 84]

1897: *Monobothrium hexacotyle*	Linton	1897: 423–456
1923: *Caryophyllaeous hexacotyle*	Woodland	1923: 451, 457
1922: "*Monobothrium*" *hexacotyle*	Nybelin	1922: 123–124
1925: *Monobothrium hexacotyle*	Moghe	1925: 23
1926: *Caryophyllaeus hexacotyle*	Woodland	1926: 56
1927: *Glaridacris hexacotyle*	Hunter	1927: 20

Specific diagnosis: With characters of genus. Adults 8 to 18 mm. long by 1.03 to 1.2 mm. wide. Ridges between six loculi form a conical apex. There is a small neck as vitellaria and testes extend to base of scolex. Body flattened dorso-ventrally, tapering posteriad; in cross section posterior end appears serrated. Cuticula 3 to 5 μ thick; subcuticula and cortical parenchyma nearly indistinguishable but 5 to 8 μ and 12 to 42 μ thick, respectively. Inner and outer longitudinal muscles present; the latter appear as scattered strands in neck. Oblong, irregular testes numbering 175 to 200; maximum diameter 0.14 to 0.26 mm. Cirrus sac occupies about one half of medullary parenchyma, maximum diameter 0.168 to 0.228 mm.; muscles of organ are 14 to 26 μ thick. Male and female reproductive systems open into a shallow, common genital atrium; female is 10 to 26 μ posterior to that of male. Vagina is convoluted, ventral, and forms distinct receptaculum seminis, 60 by 24 μ. Wings of ovary have a maximum length of 0.8 to 0.9 mm. and width of 0.096 to 0.122 mm. Ovarian commissure "V" shaped, maximum diameter 0.21 mm. Vitellaria with maximum diameter of 0.21 mm. confined to two lateral fields; do not surround the testes. A single duct drains a group of post-ovarian vitellaria. Excretory canals vary between 8 and 10 pairs ending in terminal vesicle 48 by 24 μ. Parenchyma filled with large number of irregular, glandular appearing cells which pack the medullary parenchyma from the base of the scolex posteriad, gradually thinning out as cirrus sac is reached. Specialized muscle of transverse and dorso-ventral sets form circular muscles just internal to inner longitudinal muscle mass. Eggs, ovoid, 37 to 41 by 23 to 30 μ.

Host: Catostomus sp., Gila and Salt Rivers, Arizona. In intestine.
Paratype: Specimens in Vial No. 4793 of the United States National Museum, Washington, D. C.

Host	Locality	Collector	Authority
Catostomus sp.	Gila and Salt Rivers, Ariz.	——	Linton 1897: 423–456 Hunter (the present paper)

This species was originally described in a very superficial manner, by Linton (1897) as *Monobothrium hexacotyle*. The material was secured by him from the United States National Museum at Washington, D. C. Through the kindness of the United States National Museum a vial of the original material was sent to Professor H. B. Ward. The label in the vial reads as follows "U. S. N. M. #4793. *Monobothrium hexacotyle* Linton. From sucker of Gila River and Salt River, Ariz." Since the original description does not contain a detailed account of the internal anatomy a full discussion will be given in the following pages.

Glaridacris hexacotyle is a parasite of moderate length and presents a rather montonous appearance in external view. There is but a slight widening of the scolex and practically no neck. The length of mature individuals ranges between 8 to 18 mm., while the maximum width of the specimens varies between 1.03 and 1.23 mm. The scolex appears conical even in the contracted state. The base of the scolex is nearly circular, but is divided laterally to form two lobes, one of which projects laterally from the dorsal surface and the other from the ventral. In other words the circle is broken laterally by two indentations which divide the body into dorsal and ventral halves. Each of these lobes is divided by two longitudinal ribs into three loculi, all of which meet at the apex of the scolex to form the conical papilla which may be elongated and then retracted(Fig. 3). The scolex is widest at the base; measurements of the scolices available give a width of 0.507 to 0.608 mm., while the length, taken posteriorly, varies between 0.507 and 0.608 mm. However it should be noted that there is probably more variation in living material for all the scolices were fairly well contracted. When viewed laterally the scolex was narrower and measured between 0.405 and 0.758 mm. In side view it forms a single cone, for the loculi are not readily visible from this position. The neck is very short and shows little differentiation in this species. The width at the narrowest place is between 0.455 and 0.758 mm. while the length posteriorly is 0.2 to 0.3 mm. The body possesses a maximum width of 1.03 to 1.23 mm. and is flattened dorso-later-

ally to a depth of 2 mm. It becomes narrower as the more posterior portions of the parasites are reached. The body width just anterior to the cirrus sac ranges between 0.70 and 0.86 mm. while posteriorly this decreases to 0.60 and 0.76 mm. In the posterior region there are protrusions which are caused by the distended egg-filled uterus. The posterior body tip is bluntly rounded. In several specimens it was possible to secure measurements of extended cirri. These measurements did not exactly coincide with those secured by Linton (1897:427). The extended cirri measured about 0.45 mm. in length, while the width varied from 0.02 to 0.03 mm. at the apex to 0.06 to 0.07 mm. at the base.

The internal organization of this parasite marks it as one of the most unique which have come under my observation. The scolex resembles *G. catostomi* in general shape, but a more careful examination shows it to be markedly different. The base of the scolex appears in cross section to be merely a widening of the neck region. The inner longitudinal muscles which encircle the glandular-like medullary parenchyma become pushed outwards by the swelling parenchymal mass. At this point the inner longitudinal muscles become collected first into two large "V" shaped bundles with the base of the "V" near the lateral wall. These are separated into 8 regions which roughly correspond to the 4 ridges dividing the loculi (Fig. 20). There is also a group on each side of the lateral groove at the base of the scolex. In sagittal and frontal sections it is possible to trace the distribution of these fibers with considerable ease. The bulk of them form the four central groups of muscles, but after running through the ridges between the loculi become largely dissipated and disappear in the basement membrane of the more proximal loculi. A few of the fibers and the bulk of those in the lateral fields pass to the apex of the scolex (Fig. 21).

The presence of dorso-ventral fibers running between the surfaces of the loculi tends to keep this region from expanding (Figs. 19, 21). Similar muscles running at right angles extend through the scolex laterally. (See Figs. 19-21.) Furthermore, there are a few muscle fibers extending in an anterior-posterior direction through the base of the scolex; these keep the base from elongating anteriorly.

The glandular-like medullary parenchyma gives way to the more typical cortical type filled with nuclei and the canals of the excretory system. Here again, as described for *M. ingens* and *C. terebrans*, there are extensions of the ascending canals of the excretory system into the scolex where they break down in the more distal extremities to small canaliculi which freely anastamose. The action of the fluid in these canals is no doubt responsible in a large degree for the extension of the scolex. The presence of numerous cross muscle fibers insures the elongation of the scolex when the fluids pass into the excretory canals by preventing a slight lateral distension.

The integument of this species has not been well preserved and in many

instances the outer layer of the cuticula is absent. The cuticula of this species normally possesses a thin outer membrane, less than 1 μ in thickness. Beneath this lies the thicker cuticula proper which is bounded internally by the basement membrane. The circular muscles of the cuticula may be seen in most sections as a very thin band lying just median to the basement membrane. The longitudinal cuticular muscles are more readily distinguished; they lie 2 or 3 in a fasciculus close beneath the circular layer.

The parenchymal muscles of this form are unique and will be considered in the later paragraphs dealing with the musculature. Suffice to say here that the inner longitudinal muscles are not as highly developed as in most forms while the appearance of a few circular muscle fibers complicates the structure. With the presence of these muscles and an increase in the dorso-ventral and lateral musculature there is a coincident decrease in the development of the muscles of the longitudinal system.

This species is further peculiar in that there is no apparent subcuticular layer. The canals of the excretory system which are usually found only in the cortical parenchyma are present close to the cuticula. Furthermore, the median edge of the subcuticula is normally bounded by the outer longitudinal muscles and this band is present only as a few scattered single fibers. The nuclei have the appearance typical of the subcuticula. The scattered outer longitudinal fibers are 4 to 7 μ from the longitudinal cuticular muscles and 8 to 10 μ from the basement membrane. This entire mass resembles one layer more than two and therefore will be considered as a single layer composed of the subcuticula and the cortical parenchyma. The inner longitudinal muscles are more median in the region of the scolex making the combined subcuticula and cortical parenchyma wider than it is in the posterior portions. It contains the main canals of the excretory system as well as the great mass of dorso-ventral, lateral and a few diagonal muscle fibers.

The medullary parenchyma possesses fewer parenchymal cells and contains a great mass of glandular-like cells. These are more profuse in the neck; they are large and regular in shape, measuring 24 to 60 μ by 24 to 36 μ in width, and extend from the neck posteriorly as far as the center of the body. Here their numbers begin to decrease. The testes and vitellaria invade this tissue and reduce the reticulum to a mass lying between and surrounding the organs of reproduction (Fig. 21). The testes and vitellaria are confined to the medullary parenchyma by the inner longitudinal muscles.

The musculature of this species is remarkable because of the unusual development of the smaller muscles of the parasite, coupled with the apparent degeneration of some of the prominent muscles. The cuticular system is poorly developed and has been described in the paragraphs dealing with the integument. The muscles of the parenchymal system are usually highly developed and readily discernible both in toto and sectioned

material. In the case of this parasite, however, the outer longitudinal muscles are only faintly visible and appear as single muscle fibers 8 to 10 μ from the basement membrane. The inner longitudinal muscles also lie relatively close to the cuticula. This system of muscles is between 21 and 45 μ from the cuticula; these muscles are more median in the anterior portion before they are pushed laterally by the reproductive organs.

Close to, and intermingling with, the inner longitudinal muscles are fibers from the dorso-ventral and lateral systems. These fibers, as the name implies, extend from the dorsal to the ventral surfaces of the basement membrane in which they are embedded. The lateral fibers are similarly arranged. Some of these fibers in passing the inner logitudinal muscles give off branches to this system and a few may be found extending at right angles to the inner longitudinal mass as circular muscles. This is not typical except in the middle of the body where these fibers form a layer of circular muscles lying close to those of the inner longitudinal system. The muscles passing through the inner muscle mass divide when they come within a few micra of the longitudinal muscles in order to pass between them to their insertions on the basement membrane.

Specialized muscles are also present. In the scolex the longitudinal cuticular muscles become specialized and aid in the retention of the shape of the scolex. These muscles are particularly plentiful in the loculi where they extend from the basement membrane of one across to a similar position on the loculus directly opposite (Fig. 19). A few of these fibers are also encountered in the ridges between the loculi, although the bulk of the musculature of these may be traced to the inner longitudinal muscles. These have been described in detail in the portion of this paper treating the scolex. Other specialized muscles occur in the usual portions of the reproductive system and a detailed account of them will be found in the later paragraphs.

The excretory system of *G. hexacotyle* is typical of this group of Cestodaria. There is a series of main ascending and descending canals; smaller canaliculi go to form the main ascending ducts and these canaliculi are in turn formed by the renal corpuscles or flame cells. In the scolex the ascending canals break up only to form the descending canals.

The main descending canals enter an excretory bladder or vesicle in the posterior part of the body behind the post-ovarian vitellaria. The canals enter the vesicle from all sides near the anterior lateral portion. At this point, which is the widest of the bladder, the vesicle measures 48 by 24 μ. As the exterior is approached the cavity becomes narrower until it is only 19 by 14 μ or less. This excretory bladder may therefore be described as pyriform. The length of this vesicle is between 45 and 55 μ. The bladder is surrounded also by cuticular muscles and this fact demonstrates that it is not a true pulsating excretory vessel as one finds in the trematodes.

The material is in such poor condition that no attempt will be made to work out the nervous system. Two lateral nerves show in cross section in the base of the scolex.

The male reproductive system is typical of the Caryophyllaeinae and is confined to the medullary parenchyma throughout. The various components of the system will be considered in their natural sequence. The testes are large and numerous and are confined to the field between the rows of vitellaria which in this species are entirely lateral. As might be expected the inner longitudinal muscles surround the vitellaria and the testes. In cross section these glands are flattened somewhat dorso-ventrally, and are present in 2 dorsal and 2 ventral rows, although anteriorly there are 3 rows. In size they measure between 0.144 and 0.264 mm. long, and 0.072 to 0.199 mm. wide, and number in the adult between 175 and 200 (Fig. 42). This figure was checked by an estimation of the number of testes present followed by an actual count.

The vas deferens is indistinguishable in the most anterior portions of the parasite. It first appears about one-half the distance to the cirrus sac as a small winding duct lying in the center of the medullary parenchyma. This gradually increases in size until the vas deferens becomes gorged with spermatozoa. About this time the testes disappear, first the median ones and later those on the side, leaving the entire medullary field, with the exception of the vitellaria at the lateral margins, to the coils of the vas deferens which become more dilated posteriorly. These reach a maximum diameter varying between 36 and 50 μ, although the latter figure is more typical. After numerous convolutions this structure approaches the median dorsal surface. Here it passes into the narrow, muscular ductus ejaculatorius, which continues in a posterior direction. Shortly this duct expands into an enlarged portion, the seminal vesicle. This structure is prominent and well set off from the remainder of the duct. The vessel is lined with a cuticula-like substance and this is surrounded by a layer of circular muscles intermingled with a few longitudinal fibers. The seminal vesicle narrows, dips ventrally and passes into the cirrus sac. The total length of the ductus ejaculatorius including the seminal vesicle is about 0.21 mm. The vesicle has a maximum length of 0.19 mm. and a width of 0.96 mm. and the cavity ranges between 0.146 and 0.156 mm. by 0.048 to 0.060 mm. The circular muscles form a layer which varies from 9 to 24 μ in thickness. The measurements include the young adults, for both young and old sexually mature material was studied.

The nearly round, prominent cirrus sac lies on the ventral surface directly beneath the ductus ejaculatorius and seminal vesicle, and occupies about one half the medullary parenchyma. The ductus ejaculatorius enters from the median dorsal surface. The cirrus sac has a maximum diameter of about 0.228 mm. The younger adults had cirrus sacs which measured

only 0.168 mm., even though the worms were fully developed and sexually mature. However, the thickness of the musculature was identical in both cases and measured between 14 and 26 μ. The cirrus was not extruded but the canals of the cirrus sac were evident as was the serrated inner canal of the retracted cirrus (Fig. 41). The cirrus sac opens flush with the ventral surface of the parasite, and the female system empties in a similar fashion just behind that of the male.

The vitellaria are unusual because they do not completely surround the testes, but instead lie in two lateral fields with the testes between. The inner longitudinal muscles extend about the testes and vitellaria (as in other members of the Caryophyllaeinae). The two lateral fields extend posteriorly until nearly opposite the cirrus sac. There is also a group of post-ovarian vitellaria which lie between the oötype and the excretory vesicle. These glands have a maximum diameter of 0.21 mm. The vitelline ducts from the anterior vitellaria run posteriorly through the medullary parenchyma. After the cirrus sac is passed these ducts run laterally and then medianly by the ovary so that they pass on the inner side of it. These canals swell lightly to form vitelline reservoirs and then dip ventrally, first uniting, and passing under the ovarian commissure. Here it is joined by the single vitelline duct from the post-ovarian vitellaria. This canal arises from the central portion, passes anteriorly and to the left, dipping ventrally to join the single main vitelline duct from the anterior. This single vitelline duct empties into the fertilization chamber, or vaginal-oviducal canal, just behind the juncture of the oviduct with the vagina (Fig. 41).

The ovary is lobate, "H" shaped and possesses no unusual characteristics. The main limbs of the ovary measure between 0.8 and 0.9 mm. in length by 0.096 to 0.122 mm. in width. The ovarian commissure instead of extending straight across from one wing to the other is "V" shaped, with the apex of the "V" posterior. The median portion of the commissure forms a fairly distinct ovarian reservoir which measures about 0.21 by 0.14 mm. The poorly defined oöcapt extends 10 μ from the ventral surface of the reservoir and measures from 12 to 15 μ in diameter to about 10 to 11 μ in length. The muscles are not as clearly marked as in other species. The remainder of the canal is the oviduct and is less than 15 μ in length.

The female genital atrium lies behind the cirrus sac of the male system. It follows the curves of the cirrus sac from its nost posterior position, ventrally and anteriorly until it opens on the surface 20 to 26 μ behind that of the male. The total length of this duct from its most dorsal portion, which is the beginning of the vagina, to the surface, varies between 0.24 and 0.26 mm. The uterus empties into the female cloaca from the right side, 0.16 to 0.19 mm. from the distal end of the atrium. The

female cloaca continues dorsally from the point of entrance of the uterus for nearly 0.07 mm. before it turns posteriorly to form the vagina.

The vagina in this species winds posteriorly making numerous convolutions, the majority of which are in a dorsal-ventral direction. As the ovarian commissure is reached the canal passes dorsally to a position above it. Here the vagina becomes enlarged to form a small but distinct receptaculum seminis measuring about 60 by 24 μ in cross section. Upon resuming its normal size, a diameter of less than 20 μ, the vagina comes to lie close to the walls of the ovarian reservoir. It is now surrounded by a cellular layer in which are found circular muscles. The duct passes ventrally near the posterior edge of this structure until close to the ventral surface where it doubles back upon itself to join the oviduct. The entire length of the oviduct, including the oöcapt, is between 25 and 30 μ (Fig. 84). The combined oviducal-vaginal canal forms the fertilization chamber which passes dorsally and then sweeps posteriorly in a semi-circle where the common vitelline duct joins the fertilization chamber to form the uterus. The oötype surrounds the aforementioned structures.

The convoluted uterus leads posteriorly where the thin walled portion of the egg filled uterus is found. The characteristic uterine glands do not appear until the main ascending limb is opposite the posterior portion of the ovary. Here the unicellular uterine glands appear and the uterus winds medianly and dorsally over the ovarian commissure whereupon the typical coils and convolutions form. These now extend anteriorly to the cirrus sac, and empty as already described into the female cloaca (Fig. 41). The eggs of this species are ovoid and measure between 37 and 41 μ in length by 23 to 30 μ in width. The shell is about 1 μ in thickness and appears non-operculate.

Glaridacris hexacotyle was the second species to be described from North America. Linton (1897) placed this parasite in the genus Monobothrium. It clearly belongs in the Caryophyllaeidae and falls into the Caryophyllaeinae on the basis of the medullary vitellaria surrounded by the inner longitudinal muscles. Because of the three loculi on the scolex and the presence of an external seminal vesicle this form is barred from the genus Caryophyllaeus. Furthermore in the latter genus the vitellaria are arranged annularly and in *G. hexacotyle* they are confined to the more lateral portions of the medullary parenchyma. *G. hexacotyle* differs from the genus Monobothrium in the type of genital atrium and the scolex which normally possesses the hexagonal shape and the characteristic introvert. In respect to the character of the three pairs of loculi it resembles the genus, Hypocaryophyllaeus, but in this genus the uterine coils are anterior to the cirrus sac and occupy only one fourth or less of the space taken by the testes. It therefore cannot be placed there. The possession of the three loculi places it in the genus Glaridacris which is characterized by the possession of three

pairs of loculi or bothria. The type of genital atrium, ovary, position of uterine coils, presence of post-ovarian vitellaria and external seminal vesicle clearly mark it as belonging to this genus.

In the genus Glaridacris there are two other species, both from the same host, Catostomus. The scolex of *G. laruei* is of the "Π" type, while the scolices of *G. catostomi* and *G. hexacotyle* are very similar, except that the latter is typically conical while the former is broader at the tip and does not have the loculi uniting to form a conical apex. The cuticula of *G. catostomi* is two to three times as thick as that found in *G. laruei* and *G. hexacotyle*, and the number of testes clearly sets this latter species off from the others as does the anterior vitellaria which are arranged in two distinct ununited lateral fields. In *G. catostomi* the cirrus sac occupies all the medullary parenchyma compared with one-half the medullary parenchyma in *G. hexacotyle*; in the former cirrus sac muscles have a diameter of 43 to 48 μ while those of *G. laruei* and *G. hexacotyle* measure respectively 16 to 21 μ and 14 to 26 μ. These two are alike in that a common genital atrium is lacking or inconspicuous while the female atrium lies respectively 11 to 19 μ and 20 to 26 μ posterior to that of the male. Two of these species, *G. hexacotyle* and *G. laruei* form distinct seminal receptacles in the posterior portion of the vagina. The ovaries vary somewhat in maximum length, as do the ovarian commissures. Perhaps the most significant difference is the "V" shaped ovarian commissure found in *G. hexacotyle*. The oöcapt, diameter of the ovarian commissure, and length of the oviduct all constitute differences of minor importance, while the peculiar lateral position of the vitellaria in *G. hexacotyle* as compared with the arrangement in other species is of greater import. Also in all species of this genus except *G. hexacotyle* the expanded common vitelline duct forms the reservoir. However in this latter species the several vitelline ducts expand and serve as reservoirs for the vitelline material. Lest it be argued that such a condition would occur normally let me call attention to the fact that these ducts are usually small, 10 to 15 μ or less in diameter, and are not possessed of walls that would permit expansion to a vitelline receptacle measuring four or five times as great. The eggs of *G. laruei* and *G. hexacotyle* are closely allied and measure 39 to 42 μ by 26 to 30 μ and 37 to 41 μ by 23 to 30 μ respectively. *G. catostomi* has eggs which measure 54 to 60 μ by 38 to 48 μ. The type of matrix found in the medullary parenchyma is also peculiar to *G. hexacotyle* alone. These differences serve to show beyond question the validity of this species.

GLARIDACRIS LARUEI (LAMONT 1921)

[Figs. 4, 36, 49, 50, 78]

1921: *Caryophyllaeus laruei*	Lamont	1921: 1– 4
1924: *Caryophyllaues laruei*	Johnston	1924: 347
1927: *Glaridacris laruei*	Hunter	1927: 20–21

Specific diagnosis: With the characters of the genus. Adults up to 9.5 mm. long by 0.95 mm. wide. Parasite characterized by prominent scolex about 0.4 mm. long, bearing 6 loculi and terminal disc, forming the "II" type. Disc measures about 0.06 mm. in thickness and scolex has maximum width below terminal disc of 0.55 mm. Neck distinct, having a maximum width of 0.96 mm. Body oval to cylindrical in cross section, not readily separated into subcuticula and cortical parenchyma which together measure 40 to 55 μ in thickness. Both inner and outer longitudinal muscles present, latter only indistinctly in neck region. Testes irregularly ellipsoidal, numbering between 60 and 85, 0.12 to 0.18 mm. in maximum diameter. Cirrus sac small, circular occupying about one-half of medullary parenchyma. It has a diameter of 0.108 to 0.120 mm. and the circular muscles vary between 16 and 21 μ in thickness. True genital atrium is absent and reproductive systems open on the ventral surface 12 to 19 μ behind each other. Vagina median, ventral, moderately convoluted and forms a distinct receptaculum seminis which measures 0.096 by 0.072 mm. Wings of ovary are 0.5 to 0.7 mm. long and 0.05 to 0.55 mm. wide. Vitellaria do not completely surround testes and have maximum diameter of 0.1 to 0.2 mm. by 0.03 to 0.05 mm. Excretory system composed of 8 pairs of excretory canals and terminal excretory vesicle measures 45 by 24μ. Eggs ovoid, non-operculate and measure 39 to 42 μ by 26 to 30 μ.

Host: *Catostomus commersonii*, Green Lake and Lake Mendota, Wisconsin; Douglas Lake, Michigan. In intestine.

Type: Slide No. 197 in Museum of Zoology, University of Michigan, Ann Arbor, Mich.

Paratype: Slide No. 13.16 in the collection of Dr. Henry B. Ward.

Host	Locality	Collector	Authority
Catostomus commersonii (Lacépède)	Green Lake and Lake Mendota, Wis.	A. S. Pearse	Lamont 1921: 1–4 Hunter (the present paper)
Catostomus commersonii (Lacépède)	Douglas Lake, Mich.	G. R. La Rue	Hunter (the present paper)
Catostomus commersonii (Lacépède)	Douglas Lake, Mich.	A. R. Cooper	Hunter (the present paper)

This species was imperfectly described by Miss Lamont (1921). Through the kindness of the University of Michigan Museum it was possible to obtain the original type specimen for comparison and study. This was the

only material which they had, and it was not in the best state of preservation. The same species, however, was obtained from *Catostomus commersonii* taken from Douglas Lake, Michigan by both Drs. G. R. LaRue and A. C. Cooper, and this material furnished ample specimens so that the description could be completed. Lamont (1921) secured her material from *Catostomus commersonii* taken from Green Lake, Wisc. She states that one specimen contained 24 individuals of this species and that two of the suckers from Lake Mendota, Wis. were also infected with this parasite.

The body of this parasite measures between 5.2 and 9.5 mm. in length and possesses a maximum width of 0.85 mm. The worm is flattened dorsoventrally and shows but slight changes in width. The vitellaria are confined to the more lateral portions the testes lying median to them. In the posterior fifth of the body is found a part of the male and the female reproductive system. In a specimen measuring 5.2 mm. in length, the type of "*C.*" *laruei*, the maximum width was 0.73 mm. and the distance from the tip of the scolex to the first vitellarium was 0.96 mm. The neck measured only 0.42 mm. in width. Posteriorly the body widens slightly until just before the region of the cirrus sac, where it narrows to about 0.6 mm. and behind the sac the body width drops to 0.5 mm. and then tapers posteriorly to the distal end of the body. Measurements of other specimens of this species show that these figures are typical. The table gives the maximum and minimum encountered in a study of fifteen specimens.

Length	4.2 –9.5 mm.
Maximum width	0.5 –0.95
Width of neck	0.4 –0.55
Width of body anterior to cirrus sac	0.5 –0.6
Width of body posterior to cirrus sac	0.45 –0.55
Maximum width of scolex	0.5 –0.6
Maximum length of scolex	0.3 –0.75
Width of base of scolex	0.45 –0.59
Thickness of terminal disc of scolex	0.058–0.065

The scolex is a well defined structure and appears to be characteristic for the species. The base is considerably wider than the apex, which is a flattened disc. This disc measures about 0.06 mm. in thickness and may be elevated or depressed. Beneath the disc are the irregularly marked loculi, called "poorly defined suckers" in the original paper. There are 6 loculi present. The inner longitudinal muscles extend anteriorly into the scolex and are inserted on the lateral portions of the terminal disc, thereby forming with the disc the Greek letter "Π" so evident in toto mounts. The maximum width of the scolex is below the terminal disc which measures about 0.55 mm. (Fig. 4).

The cuticula is narrow and measures between 2 and 3 μ in thickness. It

is bounded internally by a very thin basement membrane which is less than 1 μ thick. Beneath this lie the characteristic circular and the longitudinal cuticular muscles. The former lie beneath the basement membrane and the latter are scattered in bundles close to the circular layer. One or two are grouped together in a bundle.

The musculature of this species is quite typical of the Caryophyllaeinae and is composed of inner and outer longitudinal muscles. The fibers of the outer longitudinal muscle system are infrequently found in the neck region where they lie 7 to 10μ under the basement membrane. In the more posterior parts of the body this outer layer becomes lost. The distinct muscles of the inner longitudinal system are found 40 to 64 μ from the cuticula separating the cortical and the medullary parenchyma. Beneath this muscle layer lie the vitellaria which are arranged annularly about the testes. More than 10 individual muscles are found in each fasciculus which in frontal sections lie so close to each other as to form a muscular sheet. In the posterior region the muscles of the inner longitudinal system are pushed towards the surface by the distended organs of the reproductive systems notably the uterine coils.

Special musculature was apparent only in the case of the cirrus sac, seminal vesicle and ductus ejaculatorius in the male system. The cirrus sac muscles measured 16 to 21 μ in thickness while those of the seminal vesicle were only 10 to 12 μ. The walls of the ductus ejaculatorius were surrounded with a thin layer of circular muscles. Those of the other regions will be described as they are encountered.

The excretory system shows 8 pairs of canals, ascending and descending. The latter are more median and the former are composed of numerous smaller canaliculi which in turn doubtless take their origin from renal corpuscles or true flame cells, depending upon the type present. Anteriorly the canals of the ascending system send a few canals into the scolex which do not anastomose freely but turn posteriorly to form the descending canals which empty into the excretory vesicle at the posterior tip of the body. This vesicle is surrounded by deep staining myoblastic cells. Some of the fibers of the inner longitudinal muscles are embedded in the walls of this vesicle. This bladder measures about 45 by 24 μ; the canals of the excretory system empty radially at its anterior end. The vesicle opens posteriorly and ventrally.

The testes are usually arranged in two rows, although sometimes only one is found and occasionally there will be three rows. In such cases the third is ventral to the other two. These glands are surrounded laterally by the vitellaria, which usually extend well over the dorsal and ventral surfaces nearly enclosing the testes in a ring. The long axis of each testes is generally lateral, though some lie in an anterior-posterior plane. There are about 70 testes in an adult. This number when checked by actual count

and the system of estimation outlined on page 11, showed that the range is between 60 and 85. In shape these glands are globular and lobate their size ranging between 0.12 and 0.18 mm. in length and 0.072 to 0.12 mm. in width. The average length based upon the measurements of 25 testes is 0.146 mm. and the average width is 0.085 mm. (Fig. 49). The convoluted vas deferens becomes visible in between the two rows of testes in the last two fifths of the body, the testes ending nearly 0.2 mm. anterior to the cirrus sac. It was noted that although the loosely coiled vas deferens was filled with spermatozoa it was not distended. It has a maximum diameter of 25 to 30 μ and is confined to the ventral portions of the medullary parenchyma. After making several convolutions it passes ventrally and empties into the narrow muscular ejaculatorius at the seminal vesicle (Fig. 36). The seminal vesicle is relatively small and was mistaken for the cirrus by the original describer. This statement is based on the structure labelled "cirrus" on the original plate which has the same position and shape as the combined seminal vesicle and ductus ejaculatorius. As in the case of other seminal vesicles the cavity is lined with a smooth membrane about which lie the circular muscles; these measure 12 to 14 μ in thickness. This vesicle has a length of 0.079 mm. and a width of 0.048 mm. The ductus ejaculatorius leaves dorsally and is about 60 μ in length emptying into the cirrus sac from the anterior dorsal surface. It is lined throughout with circular muscles of the same thickness as those surrounding the seminal vesicle. This marks the duct as unusual, for it is more typical to find the musculature of the canal thinner than the layer about the seminal vesicle. Furthermore, the ductus ejaculatorius is long, for it measures between 130 to 140 μ in total length after leaving the seminal vesicle, and extends for 10 to 15 μ from the anterior side of the vesicle (Fig. 36). The cirrus sac lies near the ventral surface and appears somewhat ovoid measuring about 0.108 mm. in width and 0.12 mm. in greatest diameter. This difference is probably due to the pressure of the cover slip in the toto mount, for in sectioned material the vesicle appeared nearly round. The musculature varies between 16 and 21 μ in thickness. The cirrus occupied the lower half of the cirrus sac and a few retractile muscle fibers extending from the distal wall of the sac to parts of the cirrus. The cirrus does not open into an atrium, but instead it opens even with the surface about 12 to 19 μ anterior to a similar pore of the female reproductive system (Fig. 50).

The ovary is lobate and measures between 0.5 and 0.6 mm. in length and between 0.5 and 0.55 mm. in width. The ovarian commissure connecting the two arms of the ovary tapers towards the center. At this point it measures 0.05 to 0.07 mm. wide; it is 0.3 mm. from the posterior edge of the cirrus sac. The main arms of the ovary extend anteriorly as far as the posterior edge of the cirrus sac where they are nearly joined by the lateral portions of the vitellaria from the anterior part of the body.

The vitellaria lie in two lateral fields several layers deep. In the younger specimens these do not extend over the dorso-ventral surfaces to any marked degree, but in individuals over 2 mm. in length they spread out to make a ring about the testes. They are roughly rectangular in shape and measure between 0.1 and 0.2 mm. in length and 0.03 to 0.05 mm. in width. The vitellaria do not mingle with the testes, but are confined laterally about them. They are slightly more numerous in the posterior regions of the body. There is a third group, the post-ovarian vitellaria, which are found between the posterior coils of the uterus and the excretory vesicle. The vitelline ducts first appear anterior to the cirrus sac; they pass posteriorly on the inner side of the ovary and then unite to form the single vitelline duct. This canal expands distally to serve as the vitelline reservoir. It passes dorsally to the ovarian commissure and then dips ventrally into the ovarian complex where it soon joins the vaginal-oviducal canal, first connecting with a single duct from the post-ovarian vitellaria (Fig. 36).

The vagina runs posteriorly from the female cloaca and the uterus enters from the left side, 0.07 mm. from the posterior margin of the cirrus sac. The cloaca is 0.048 to 0.055 mm. in width at this point and maintains the same width until it narows near the cirrus sac. Shortly after the vagina leaves the cloaca it turns ventrally and gives way dorsally to a large receptaculum seminis approximately 0.096 mm. long by 0.072 mm. wide. The vagina then passes posteriorly and dorsally to the ovarian commissure. It follows close to the ovarian commissure and passes ventrally to enter the ovarian complex.

The oöcapt arises from the median posterior edge of the ovarian commissure and winds its way laterally into the oötype complex. The sphincter muscle controlling the release of the ova is about 6 to 8 μ thick, and the total diameter of this tube and muscular wall is between 10 and 13 μ. It extends posteriorly for 10 μ before it gives rise to the less muscular oviduct which unites with the vagina to form the oviducal-vaginal canal, or fertilization chamber. Less than 7μ from the juncture of these two canals the vitelline duct unites to form the uterus (Figs. 36, 50). The uterus coils through the small oötype and then passes posteriorly. The uterus is thin walled until the anterior limb of the uterus is opposite the posterior arm of the ovary. At this point the unicellular uterine glands appear and completely surround the uterus. The function of these cells is not known. The convolutions of the uterus do not pass anteriorly to the cirrus sac and after several twists empties into the female genital atrium from the left side. The uterus was filled with eggs, some of which retained their original shape. These were non-operculate and possessed a moderately thin shell beneath which were heavy enveloping membranes. The eggs were small, nearly oval and measured between 39 and 43 μ in length and 25 and 31 μ

in width. The average size based upon 20 eggs was 40.9 μ by 28.95 μ.

The material which furnished the basis for the original description of this parasite was secured from *Catostomus commersonii*, Lacèpéde, taken from Lake Mendota, Wisconsin on August 22, 1919 and Green Lake, Wisconsin on August 25, 1919. Miss Marion E. Lamont described this helminth. The description was extremely inadequate as she was apparently unaware of the existence of papers already published in this country, notably that of Cooper (1920) and those of Linton (1893, 1897).

Sometime later some Cestodaria from *C. commersonii* also taken from Lake Mendota were sent to Dr. Cooper for identification. He determined them as being *G. catostomi* which he had described in 1920. A careful study of Cooper's material and the type specimen of "*G.*" *laruei* from the University of Michigan Museum, as well as the slides sent to Dr. Cooper for identification by Dr. Pearse, shows that "*C*" *laurei* and *G. catostomi* are not identical. In order to ascertain this beyond question the author went to Lake Mendota, Madison, Wisconsin to secure additional material. But even though Professor M. F. Guyer was extremely kind and other members of the staff furnished nets, etc. it was impossible to secure any more infected fish. Fortunately, however, Cestodaria belonging to this species were subsequently found in collections of Drs. G. R. LaRue and A. R. Cooper from Douglas Lake, Michigan which enabled me to ascertain the validity of the species.

This species readily falls in the Caryophyllaeinae and by virtue of the type of scolex may be placed in the genus Glaridacris. The scolex characteristic for this species has been described as the "Π" type and differs from *G. hexacotyle* in not being pointed distally and from *G. catostomi* in not being wedge shaped. Both lack the terminal disc so characteristic of this species. It resembles *G. hexacotyle* and *G. catostomi* in the possession of 6 rather than 4 loculi as recorded by Lamont (1921:2). The matter of this type of scolex will be considered in detail later. The cuticula of *G. laruei* measures between 2 and 3 μ in thickness and this is thinner than that found in any of the other species, for *G. hexacotyle* and *G. catostomi* have a cuticula measuring 3 to 5 and 7 to 11 μ respectively. That this layer of *G. laruei* is simply thinner because it is younger may be answered by pointing to the larvae of *G. catostomi* where the cuticula was found to be about 25 μ in thickness. In other words the thickness of the cuticula, at least in *G. catostomi*, appears to be inversely proportional to its age and size. The outer longitudinal muscles are not as distinct as in *G. catostomi* where they stand out with great clarity. In fact in many of these species the outer longitudinal muscles are so poorly developed as to be almost absent. The testes in *G. laruei* number between 60 and 85 as compared with 175 to 200 and 405 to 420 for *G. hexacotyle* and *G. catostomi*. These glands are completely surrounded by the vitellaria in all

cases except *G. hexacotyle* where they are confined anteriorly to two lateral rows and *G. laruei* in which the vitellaria nearly surround them. In the latter species the cirrus sac is small, circular, occupying only one half of the medulla and has a maximum diameter of 0.108 to 0.120 mm., the smallest yet recorded. In *G. laruei* the male and female reproductive systems do not open into a common genital atrium, but instead open even with the surface behind one another. In contrast to this condition is *G. hexacotyle* with an atrium of 3 to 5 μ in depth and *G. catostomi* whose common genital atrium measures between 0.7 and 0.15 mm. in depth. The female reproductive systems open 12 to 19 μ posterior to that of the male in *G. laruei*. In all the other members of this genus this distance is vastly greater, with the exception of *G. hexacotyle* in which the distance is 20 to 26 μ. Once more *G. catostomi* may be separated from *G. laruei* on the basis of size of eggs, for in this species they are 15 to 20 μ larger than those of *G. laruei*. The latter, however, has the same size eggs as *G. hexacotyle*, measuring respectively 37 to 42 by 23 to 30 μ. One difference, however, is apparent, for the embryos of *G. laruei* are surrounded by a thin outer shell under which lies a heavy enveloping membrane not found in the eggs of *G. hexacotyle*. Furthermore, this latter species possesses a characteristic type of parenchyma which differs from anything yet encountered.

Cooper (1920) confused specimens of *G. laruei* and *G. catostomi* (a full discussion of this occurs on page 59). It is also evident that scolices of this parasite may take several different shapes. The typical example shows the terminal disc well protruded with the three loculi situated in between the so-called "Π." How this disc becomes extruded is an interesting study, but some light is thrown on the problem from the data at hand. In the case of specimens with fully contracted scolices the terminal disc alone shows. The remainder of the scolex appears swollen laterally and microscopic examination reveals the presence of the parallel longitudinal muscles within the scolex drawn down inside by the action of the strong inner longitudinal muscles. Rarely the terminal disc is absent, evidently having disappeared by being pulled in between the bands or due to degeneration of the scolex before fixation. The former condition is indicated by 2 small humps extending distally from the rounded portion of the scolex. In such cases the width of the organ is decreased; the muscle bands are evident at this stage also. By the contraction of the muscles in the base of the scolex the circumference is decreased. Since the body cannot increase materially in width, this protoplasm, including the liquids in the excretory canals are forced into the distal portion of the scolex. In other words it is forced *between* the inner longitudinal muscle bands which form the two protrusions. Then by the action of specialized muscles the distal end flattens out and forms the terminal disc giving the typical "Π" shaped scolex which is so characteristic of this species. This

species differs from *Glaridacris confusus*, in several important respects, but likewise has some characteristics in common. Thus the adults are about the same length and typically possess the same type of scolex; furthermore the cuticula is essentially the same, and in both parasites the subcuticula and cortical parenchyma is combined in one. This layer is 15 to 40 μ in thickness in *G. confusus* compared with 40 to 55 μ in *G. laruei*. The testes number 60 to 85 in the latter and only 25 to 35 in the former, while the muscles of the cirrus sac measure respectively 16 to 21 μ and 10 to 17 μ. In both cases the reproductive systems open on the surface, the male and female pores being only 12 to 19 μ apart in *G. laruei* compared with 20 to 55 μ in *G. confusus*. In the former the vitellaria nearly surround the testes while in the new species they are confined to two lateral rows as in *G. hexacotyle*. And lastly the hosts are very different for *G. laruei* is reported only in *C. commersonii* while the latter was taken from *Ictiobus bubalus*, Ictiobus sp. and *Dorosoma cepedianum*.

GLARIDACRIS CONFUSUS HUNTER 1929

[Figs. 22, 24, 43, 66–68]

1929: *Glaridacris confusus* Hunter 1929: 189–190

Specific diagnosis: With the characters of the genus. Adults usually 3 to 7 by 0.2 to 0.8 mm., flattened dorso-ventrally. Scolex oval at base, tapers to a chisel-shaped extremity which is cut by 6 loculi. Inner longitudinal muscles are usually present drawn into four prominent and four weaker groups of fasciculi confined to lateral thirds of base of scolex; outer longitudinal muscles rudimentary. Cuticula 2 to 4 μ thick. Subcuticula inseparable from cortical parenchyma combined width of 15 to 40 μ except in neck and scolex. Medullary parenchyma occupies three fourths of body width. Testes large, 0.1 to 0.3 mm. by 0.1 to 0.13 mm. and numbering 25 to 35; they occupy two parallel rows. Cirrus sac fills one third to one half medullary parenchyma, maximum diameter 0.16 mm.; circular muscles 10 to 17 μ thick. Male and female reproductive systems open on surface 20 to 55 μ apart. Vagina forms large receptaculum seminis, "S" shaped and situated anterior and dorsal to ovarian commissure which are 0.13 to 0.27 mm. long and 0.031 to 0.067 mm. wide. Vitellaria confined to two lateral rows, 0.067 to 0.135 mm. maximum diameter. Eggs small, ovoid, 37 to 48 by 20 to 31 μ.

Host: *Ictiobus bubalus*, Rock River, Illinois and Mississippi River, Fairport, Iowa; *Ictiobus bubalus*, *Ictiobus sp.* and *Dorosoma cepedianum*, Tallahatchie River, Mississippi. In intestine.

Type: Slide No. 29.41 in the collection of Dr. Henry B. Ward.

Paratypes: Slides in the collection of the Department of Zoology, University of Minnesota.

Material in author's collection No. 642.2–642.10.

Host	Locality	Collector	Authority
Ictiobus sp.	Tallahatchie River, Money, Miss.	Parke H. Simer	Hunter (the present paper)
Ictiobus bubalus (Rafinesque)	Tallahatchie River, Money, Miss.	Parke H. Simer	Hunter (the present paper)
Ictiobus bubalus (Rafinesque)	Mississippi River, Fairport, Ia.	G. W. Hunter, III	Hunter (the present paper)
Ictiobus bubalus (Rafinesque)	Mississippi River, Fairport, Ia.	——	Hunter (the present paper)
Dorosoma cepedianum (Le Sueur)	Tallahatchie River, Money, Miss.	Parke H. Simer	Hunter (the present paper)

The material forming the basis of this description was taken by Dr. Parke H. Simer in Mississippi during the spring of 1927. In many cases the tissues appeared somewhat vacuolated. According to Dr. Simer's report he used Bouin's picro-formol-acetic or a saturated aqueous solution of mercuric chloride. Both of these fixatives should give excellent results. The reason for this supposedly poor fixation can be traced to the hosts which undoubtedly had to lie out of water exposed to the warm air for hours before they were examined. Cestodaria are particularly sensitive to such exposure and if they do not leave the host will soon decompose. It has been observed by the author that the scolex is the first region to become affected. This accounts for the apparently great diversity of shapes assumed by the scolex within the confines of a single species. Such differences do not occur in the living material and this forms one of the greatest arguments for the use and study of living specimens. The exact nature of this effect cannot be stated; whether the digestive juices which are released in quantity as the fish dies have a deleterious action upon the portion of the parasite in contact with the host, or whether the reproductive system is more resistent is not apparent. The result in either case is the same. In describing this and other species the author has endeavored to use specimens which have not undergone this degeneration.

Figure 22 shows the most common type of scolex encountered, although many variations were met.

Glaridacris confusus is relatively small, and broad. The adults when fixed measure between 3 and 7 mm. Occasionally specimens were found which measured nearly 20 mm. These all were fully matured forms as was evidenced by the presence of great numbers of eggs in the uteri. In many instances the parasites were contracted due to the action of the well developed inner longitudinal muscles. Such contraction tends to increase the breadth which varied between 0.27 and 0.8 mm. Maximum breadth occurs at the base of the scolex (Fig. 22). This organ is oval at the base, and tapers to a chisel-shaped extremity which is cut by six loculi (Figs. 66, 67). The region of the cirrus sac and uterine coils was the next widest place while the short neck universally constituted the narrowest. This latter region is hardly discernible for it gives way immediately to the body which contains the reproductive organs. Upon examining a toto from the ventral surface one is impressed by the compactness of the uterine coils which do not extend beyond the anterior limits of the cirrus sac (Fig. 24).

There are several other rather striking features characteristic of this species. The cuticula while very thin, measuring between 2 and 4 μ, is subdivided into several parts or regions. The outermost strip takes the stain less deeply than the inner and thicker portion. In some cases slight vacuolization occurred, but in these one also found a scolex undergoing degeneration. This evidence supports the conjectures made by the author in regards to the fixation of *C. terebrans* and other species. In cases of vacuolization the cuticula appeared slightly thicker, but in normal specimens the cuticula never exceeded 4 μ. It was thinner upon the scolex than in other parts of the body. The inner layer of the cuticula constitutes two thirds of the whole and takes the counter stain deeply. Beneath this and usually in contact with it, replacing the customary basement membrane, lies the thin layer of circular cuticular muscles. This is followed by the bands of longitudinal muscles. Each occupies less than 1 μ. Apparently the subcuticular layer and the cortical layer of the parenchyma have become fused into a single undivided mass. This was also the case with *G. hexacotyle*. The outer longitudinal muscles appear to degenerate for in many cases they could not be found. There is some reason to believe they may have become fused with the longitudinal cuticular muscles for some times a second mass of fibers could be discerned only a few micra from the cuticular layer. These are thought to be the remains of the outer longitudinal muscles which have degenerated. This combined subcuticula and cortical parenchymal layer is narrow and measures but 15 to 40 μ in all parts of the body except the neck and scolex where it may be 60 μ. Scattered throughout the body are a few dorso-ventral muscle fibers taking their ori-

gin from the inner longitudinal muscles. These fibers are more prominent in the region of the reproductive system (Fig. 43).

In studying a toto mount one is inclined to place the specimen amongst the Lytocestinae due to the inner longitudinal muscles. As these leave the scolex one sees in a dorsal or ventral view four rows of muscles, two on each side; the more median ones appear to run between the testes and the vitellaria (Fig. 24). A closer examination shows the spreading of these fibers into a sheet which surround the vitellaria and testes. An examination of cross sections dispels any doubts as to the disposition of these muscle layers and one is forced to the conclusion that it belongs in the Caryophyllaeinae (Fig. 68). The excretory system is characteristic of the group and presents no unusual features. In the scolex are only a few branches of the system and as the neck is reached these assume a more orderly arrangement. The number of pairs of ascending and descending canals varies but are between ten and twelve. They appear in the combined subcuticular and cortical parenchymal layer. Posteriorly they pass into a terminal pear-shaped excretory vesicle which ranges in size from 0.11 to 0.13 mm. by 0.020 to 0.030 mm. the ducts emptying into the vesicle at its widest point. It is lined with a continuation of the cuticula. Little could be seen of the nervous system except the two ganglia in the base of the scolex (Fig. 22).

The outstanding feature of the male reproductive system is the small and constant number of testes, which range between 25 and 35. They are nearly round and are packed closely together, being much larger in proportion than the vitellaria which are confined to two lateral fields. The testes measure 0.1 to 0.3 by 0.1 to 0.13 mm. and in toto mounts appear granular, taking the haemotoxylin stain as deeply as the ovary. In section they appear to be composed of a number of small globes, the margins of which are lined with cells. Thus there are a quantity of small circles, whose outlines appear stippled, going to make up the true testes (cf. *Monobothrium ingens*). These are perhaps the seminiferous tubules. The vas deferens appears about the middle of the testicular field and as the last testis is passed it fills the entire medullary field with is convolutions. After a number of lateral twists first to one side and than to the other the vas deferens narrows and assumes a median position and wanders towards the cirrus sac. It is, however, dorsal and anterior to it. Less than 0.1 mm. from the cirrus sac it dips ventrally and anteriorly passing into the muscular seminal vesicle. This structure is a large crescent shaped organ, with one end lying beneath and to the right of the cirrus sac and the other entering this organ by means of the ductus ejaculatorius on its anterior median dorsal surface (Fig. 24). It measures 0.1 to 0.3 mm. in length and 0.031 to 0.067 mm. in width. The muscular layer is between 10 and 20μ thick, being much more developed than those of the cirrus sac. The ductus

ejaculatorius is short, 17 to 23 μ long; the tube itself is but 3 to 4 μ in width while the muscular lining is 10 to 15 μ in depth. The small round cirrus sac occupying but one third to one half of the medullary parenchyma, ranges between 0.1 and 0.16 mm. in maximum diameter. The circular muscular layer is thin varying between 10 and 15 μ in width. The cirrus itself has a maximum length of 0.2 mm. and a diameter of 20 to 40μ. It is filled to its distal extremity with retractile muscle fibers (Fig. 43). The circular muscles of the cirrus sac are attached ventrally to the body wall and force the cirrus out by contraction. The male reproductive system opens via a shallow male genital atrium on the ventral surface 20 to 55 μ anterior to the female system (Fig. 24).

The female genital atrium extends dorsally and posteriorly at an angle of 30 to 45 degrees. About 0.08 to 0.13 mm. from the mouth of the tube the uterus empties dorsally and laterally; the vagina continues posteriorly through a very narrow muscular neck. This soon expands giving rise to an immense receptaculum seminis measuring 0.13 to 0.27 mm. by 0.031 to 0.067 mm. This structure arises anterior to the ovarian commissure and continues up and over it, the thin walled receptaculum seminis passing well to the left of the center of the parasite in the median plane of the body. The vitelline duct passes over the ovarian commissure and crosses between it and the receptaculum seminis (Figs. 24, 43). Posteriorly this vacuity narrows and forms a small straight duct which empties directly into the oviduct. This latter part of the vagina is surrounded by a few circular muscle fibers. The anterior vitellaria (as in the case of *G. hexacotyle*) are confined to two lateral rows. This is contrary to the situation found in most of the Caryophyllaeinae, being quite characteristic of the Wenyoninae. Several of the other Caryophyllaeinae have approached this condition. The post-ovarian vitellaria are located in the usual fashion behind the wings of the ovary. The vitelline ducts descend from the anterior vitellaria and pass either just inside (i.e. median) or dorsal to the wings of the ovary. As the ovarian commissure is reached they turn medianly and unite to the left of the center. Usually a few micra from the point where the two anterior ducts empty the post-ovarian vitelline duct joins, having closely followed the left ovarian wing (Fig. 43). The common vitelline duct is short, passing medianly where it unites with the fertilization chamber (vaginal-oviducal-canal) to form the proximal end of the uterus.

The ovary differs from many of the other members of this subfamily in that it is granular in appearance instead of globular. Usually one finds the wings divided into a number of smaller divisions and while these in turn may seem granular the ensemble appears as a number of globules. These are specific differences. The wings of the ovary vary in length from 0.4 to 0.75 mm. in length and 0.1 to 0.12 mm. in width, the connecting com-

missure being relatively narrow and having an average diameter from 0.030 to 0.12 mm. In sagittal sections the commissure appears round. The oviduct arises to the left of the center by a poorly developed oöcapt which is weakly supplied with muscles. The oviduct is straight and short being 30 to 40 μ in length and 3 to 4 μ in width. The vagina joins it in the outer limits of the oötype which is smaller than was noted in other species (Fig. 43). It loops over itself, picks up the common vitelline duct and proceeds by a tortuous route to the posterior limits of the oötype where it expands into the upper end of the uterus proper. The typical uterine glands do not appear about the coils of the uterus until the duct passes the ovarian commissure enroute to the exterior (Fig. 43). The longitudinal extent of the uterus varies between one fifth and one third of the length of the testicular field; it averages just over one fourth, 26.8 percent, in measurements of 25 specimens. Fifty eggs of this species were measured and were found to average 42 by 25μ. The actual range was from 37 to 48μ in length and 20 to 31μ in breadth. They appear ovoid, fairly thick shelled and contain an ovum and five or six globules of vitelline material.

Glaridacris confusus is placed in the Caryophyllaeinae on the basis of the appearance of the sexual apertures in the last fourth of the body length and the presence of the uterine glands and vitellaria within the inner longitudinal musculature. Since it does not possess uterine coils extending anterior to the cirrus sac it falls into one of three genera, Caryophyllaeus, Monobothrium or Glaridacris. It belongs to the latter on the basis of the type of scolex, length of the uterine coils in respect to the testicular field, the type of genital atrium and the presence of an external seminal vesicle. *G. confusus* differs from *G. catostomi*, and *G. hexacotyle* in the type of scolex, length, number of testes, size and shape of receptaculum seminis, number of excretory canals, the host and a number of minor points. It resembles *G. laruei* in the type of scolex, and differs from it in the number of testes and excretory canals, the arrangement of the vitellaria, the size and shape of the receptaculum seminis, the type of vagina and the host. A number of other differences appear upon a closer reading of the description of the forms, but these which are listed are sufficient to establish this form as a new species. It was named *G. confusus* because of its superficial resemblance to the Lytocestinae.

GENUS CARYOPHYLLAEIDES NYBELIN 1922

Generic diagnosis: Caryophyllaeinae with blunt, scarcely broadened anterior extremities, without a trace of specialization. Cirrus opens into utero-vaginal canal before it empties into the surficial atrium. Ovary with long wings, joined posteriorly behind the oötype, forming an inverted capital "A." Uterine coils anterior to cirrus sac, reaching a maximum longitudinal length of one-half to one-third that of testicular field. Terminal

excretory bladder and post-ovarian vitellaria present. No external seminal vesicle. Parasitic in the intestines of Cyprinidae. Development unknown.

Type species: *Caryophyllaeides fennica* (Schneider 1902).

To include: *Caryophyllaeides fennica* (Schneider 1902); *C. skrjabini* (Popoff 1924).

The validity of this genus was soon demonstrated by the description of "*Caryophyllaeus*" *skrjabini* by Popoff in 1924. He was apparently unaware of the excellent piece of work done by Nybelin (1922). But it was readily seen that by an elimination of some of the subgeneric characters from Nybelin's diagnosis that this parasite described by Popoff really belonged in this genus. His figures show two of the most diagnostic characters for the genus, the presence of the uterine coils anterior to the cirrus sac and the characteristic "A" shaped ovary. Motomura (1927) says that he omitted "*Caryophyllaeus*" *skrjabini* and "*Caryophyllaeus*" *fennica* because he was unable to find any specific differences between the two. Several differences of importance are evident from a superficial examination of the work of Nybelin (1922) and Popoff (1924). First of all the scolices are different, for *Caryophyllaeides fennica* possesses an unspecialized scolex while *C. skrjabini* has a few very weak longitudinal loculi (?). The latter possesses four rows of "Fäserzellenstränge" while Nybelin does not note any for the former. The testes number in *C. fennica* is about 150 while Popoff gives 83 as the maximum for his species. Furthermore judging from the descriptions and the figures the receptaculum seminis differs in the two; in *C. fennica* it runs in an anterio-posterior direction while in *C. skrjabini* it runs dorso-ventrally at an angle of about 45 degrees with the vertical. These are a few of the differences which clearly indicate the validity of the species under consideration.

GENUS BIACETABULUM HUNTER 1927

Generic diagnosis: Caryophyllaeinae with well defined scolex, varying but little in shape, bearing one pair of well defined acetabular-like suckers, with or without additional loculi. Cirrus opens into the utero-vaginal canal before it reaches the surficial atrium (like Caryophyllaeides). Ovary "H" shaped and entirely medullary. The uterine coils extend anteriorly to the cirrus sac, reaching a maximum longitudinal extent of one fourth that of the testicular field, usually less. Terminal excretory bladder and external seminal vesicle present. Post-ovarian vitellaria present. Parasitic in the Catostomidae. Development unknown.

Type species: *Biacetabulum infrequens*, Hunter 1927.

To include: *Biacetabulum infrequens*, Hunter 1927; *B. meridianum*, Hunter 1929; *B. giganteum*, Hunter 1929.

This genus has a wide distribution both as to the host and the locality. The type species was found in two specimens of *Moxostoma anisurum* (Rafinesque) which were secured through the kindness of Dr. David H. Thompson. The author had previously examined other members of the genus and found them uninfected. For example, 17 specimens of *Moxostoma breviceps* (Cope) from the same stream and general locality did not yield a single Cestodarian. During the summer of 1928 the author examined other members of the genus; these were all taken from Lake Erie. In all 6 *Moxostoma duquesnii* and 1 each of *M. aureolum*, *M. leseuri* and *M. anisurum*. None of these harbored Cestodaria. The second species was found by Dr. Fred J. Holl in *Erimyzon sucetta* from the Eno River, North Carolina. The last species was collected from both *Ictiobus bubalus* and *I. cyprinella* from various parts of the Mississippi River basin, Lake Pepin (Minnesota), the Rock River (Illinois), the Mississippi River (Iowa), and the Tallahatchie River (Mississippi). The genus was so named because of the presence of two acetabular suckers.

BIACETABULUM INFREQUENS HUNTER 1927

[Figs. 12, 16, 17, 32, 48, 69, 70, 85]

1927: *Biacetabulum infrequens* Hunter 1927: 22

Specific diagnosis: With the characters of the genus. Adults from 16 to 22 mm. in length by about 0.6 mm. in breadth. The scolex is armed with one pair of acetabular suckers 0.168 to 0.24 mm. in diameter. Neck is distinct, having a maximum length of 0.5 mm. Body oval in cross section and posteriorly appears serrated. Cuticula 4 to 5 μ thick, followed by a subcuticula layer which is 7 μ deep and the cortical parenchyma 60 to 70 μ thick. Inner and outer longitudinal muscles are present and fairly prominent in the neck. Testes irregularly oval with maximum diameter of 0.079 to 0.168 mm. and number between 420 and 440. Cirrus sac round, occupies one-third to one-half of the medullary parenchyma, with a maximum diameter of 0.144 mm. and muscles 19 to 24 μ thick. Cirrus opens into utero-vaginal canal about 0.05 to 0.8 mm. from the ventral surface. Vagina convoluted, forms a distinct receptaculum seminis 0.105 by 0.048 mm. Wings of the ovary 0.608 to 0.658 mm. long; ovary practically fills the medullary parenchyma for the ovarian commissure is broad. Vitellaria surround the testes and measure 0.084 to 0.168 mm. in length. Excretory system has 8, 10, and 12 pairs of canals which empty into an excretory bladder 0.090 mm. long by 0.024 to 0.036 mm. in width.

Host: intestine of *Moxostoma anisurum*, Rock River, Illinois.

Type: Slide No. 29.42 in the collection of Dr. Henry B. Ward

Paratypes: Slides and vials Nos. 577.2–577.8 in the author's collection.

Host	Locality	Collector	Authority
Moxostoma anisurum (Rafinesque)	Rock River, Rock Falls, Illinois	D. H. Thompson	Hunter (the present paper)

During the past six years fourteen fish from the Rock River of the genus Moxostoma were examined. Twelve were *Moxostoma breviceps* and two were *M. anisurum.* Those from the former yielded no Cestodaria while both specimens of the latter were infected with Caryophyllaeinae. About 21 parasites were collected in all from two fish. A superficial examination showed that they belonged to the same species, for the movement, arrangement of the reproductive organs and the type and action of the scolices were identical. These parasites constituted a new genus and new species, *Biacetabulum infrequens,* Hunter (1927).

Biacetabulum infrequens reached a maximum length of 30 mm. while alive; the same specimens when fixed were only 20 mm. in length. Inasmuch as no eggs were found in the uteri it is possible that these individuals were sexually immature. If such is the case live adult worms would doubtless reach a length of 40 to 50 mm. However, it seems probable they were sexually mature for the testes were fully developed, much more so than is characteristic of immature forms. Furthermore, the uteri showed the presence of globules here and there which indicate that eggs had been present. It is known that parasites of fish, particularly Cestodaria, are much less plentiful in the winter than in the summer. Therefore, since these fish were examined during the first part of December the absence of eggs may be interpreted as the most conclusive bit of evidence to support the view that the parasites were adults which had already produced their quota of eggs.

The scolex is broadened laterally and tapers to the anterior extremity so that in cross section it appears nearly rectangular. The tip in one specimen was 0.2 by 0.1 mm.; this broadens rapidly until the suckers are reached. At this point the scolex is at its maximum width. It measures 0.4 mm. broad and 0.5 mm. long. In this case the greatest length occurs in an anterior-posterior direction, tapering posteriorly into the neck (Fig. 12). The suckers are two in number, these are supplemented by four small loculi which occur on the dorsal and ventral sides only. The two suckers, opposite one another in the median plane, are the most efficacious. These are flanked by the shallow loculi which are much less conspicuous and sometimes only show in sections. The latter measure between 0.24 and

0.4 mm. in depth and 0.06 to 0.12 mm. in width. The acetabular suckers are much larger in all respects. There is considerable range as is shown by the following maximum and the minimum measurements. The depth varies between 0.07 and 0.14 mm. while the width is between 0.16 and 0.24 mm. The acetabular depressions show a marked increase of the subcuticular layer which in this region is largely composed of the longitudinal muscles of the cuticula (Fig. 16).

In sagittal section the scolex may be studied to better advantage. The tip is wider and slightly rolled so that in section it appears knob-like. This knob has a diameter of about 0.15 mm. in a normally contracted specimen. It tapers posteriorly for 0.5 mm. which at the more lateral portions gives way to a pair of small depressions. Below and median to these two pairs of small loculi are found the main adhesive organs. This pair of suckers is typically acetabular. As these are paired and therefore back to back one is reminded by them of two parentheses so placed (Figs. 16, 17). They are liberally supplied with muscles from the inner longitudinal mass most of which are concentrated in large bands at the distal portions of the sucker. The concave surface of the sucker is furnished with numerous small muscles which leave the basement membrane perpendicularly and run back into the thick mass of parenchymal cells. These cells pack the scolex solidly from the posterior edge to the apex. This mass of parenchymatous tissue is interesting in several respects. In the first place muscle fibers extend from the most anterior portion of the sucker distally until they become embedded in the tip of the scolex. Other fibers leaving the basement membrane in the middle of the sucker connect with the basement membrane of the other side opposite. This arrangement undoubtedly helps to preserve the acetabular shape and at the same time aids in keeping the scolex turgid. These muscles come from the longitudinal cuticular layer which in this region has become highly specialized. At the base of this muscle layer are a series of cavities which can be traced to the main canals of the excretory system. At the posterior edge of the large acetabular suckers the parenchyma thins out into loose connective tissue for about 60 μ. This connective tissue is penetrated rather freely with canals of the excretory system. On each side of the scolex an excretory tube runs anteriorly with the inner longitudinal muscles. Furthermore, muscle fibers of two sorts are found at the posterior tip of the main suckers. First there are circular muscle fibers which extend medianly about and behind the suckers; the fibers from both suckers meet in the median line. A few seem to turn posteriorly and become a part of the inner longitudinal muscle mass. This marks the limits of the parenchyma in the scolex. Other fibers having their insertion at the same spot run posteriorly to parallel the surface of the parasite. These become the outer longitudinal muscles which function in the contraction of the scolex. Behind the mass of loose connective tis-

sue occupying the cortical and medullary layers of the parenchyma for a length of 0.14 to 0.16 mm. are parenchymatous cells and most of the inner longitudinal muscles (Fig. 16). The lateral portions of the inner longitudinal muscles extend forward to the anterior tip of the scolex (Fig. 17). In the lateral parts of the scolex are numerous irregularly shaped cells whose function is not understood by the author. They are similar to those noted by Cooper (1920) and by the writer in *M. ingens*, etc.

The mechanism by which this type of scolex functions is interesting. It is evident that most of the contraction of the scolex is handled by the massive muscles of the inner longitudinal system. Expansion of the scolex, however, is a different story. Fluids in the canals of the excretory system if passed anteriorly reach the plexus of canals at the base of the scolex in the loose connective tissue. This causes an elongation of the entire scolex. Such a phenomenon would be aided by the three tubules extending to the distal portion of the scolex and also by the cross fibers which would keep the scolex from swelling laterally thereby forcing it to elongate. Essex (1928) has described a somewhat similar situation in Corallobothrium.

Behind the suckers the scolex begins to narrow until finally the neck is reached. This is characterized in being more oval than the testicular region; there is no sharp differentiation between the subcuticula, medullary and cortical parenchyma as is normally found. A typical specimen is really circular in cross section and measures about 0.4 mm. in diameter. As the region of the first vitellaria is reached the shape becomes more oval until it measures 0.4 mm. deep by 0.5 mm. in width. The first vitellaria appear nearly 1.3 mm. from the anterior tip in a normal adult, making the neck a rather small region averaging 0.5 mm. in length. The excretory canals are confined to the cortical parenchyma, which has now become clearly separated by the longitudinal muscles. The study of the cuticula of this species reveals that it is in essential agreement with that found in other species of the Caryophyllaeinae except that this layer is remarkably thin and measures only between 4 and 5 μ including the basement membrane. The latter, however, is less than 1 μ in thickness and is very difficult to distinguish from the cuticula proper. Beneath the basement membrane lies the narrow layer of circular muscles which become thinner posteriorly. Median to the circular cuticular layer are found the fibers of the longitudinal system. This system reaches its maximum development in the scolex where the longitudinal cuticular muscles aid in the functioning of the acetabular suckers. Four or 5 μ beneath the most median layer of cuticular muscles lie the outer longitudinal parenchymal muscles; these muscles nearly disappear posteriorly. However, they extend anteriorly and are attached to the base of the terminal disc outside the acetabular suckers. It is usual for the outer longitudinal muscles to lie

at the base of the subcuticula and to divide it from the cortical parenchyma. In this case, as in *Hypocaryophyllaeus paratarius*, there appears to be little differentiation between the two. A shallow subcuticula is marked by increased pigmentation and is followed by a deeper staining cortical layer of the parenchyma. This cortical layer is characteristic and contains the canals of the excretory system. The entire distance from the edge of the cuticula to the base of the subcuticula is only about 12 μ. When 4 to 5 micra are subtracted for the thickness of the cuticula (and when one realizes that beneath the cuticula are found two small sets of muscles), it is apparent that the subcuticula layer is little more than 7 μ in depth. The cortical parenchyma is filled with loose connective tissue and numerous parenchymal cells. This layer if measured in the middle of the body, extends medianly for 60 to 70 μ before the inner longitudinal muscles are encountered; anteriorly it is not so thick. As already mentioned this region is filled with the paired tubules of the excretory system. The musculature of the inner longitudinal mass lies about the vitellaria which in turn surround the greater portion of the testes. These muscles, lying in a nearly continuous ring about the reproductive organs, are grouped with 6 to 14 muscle fibers in a fasiculus. Anteriorly the entire neck region and the part just posterior to it are filled with the inner longitudinal muscles.

The cuticular muscles are found at the inner edge of the basement membrane, the muscles lying immediately beneath this membrane being the circular muscles. This layer extends for nearly 1 μ in depth before it gives way to the longitudinal muscles of the same system. These are grouped with one or two fibers together and are situated at irregular intervals about 0.5 to 1 μ apart at the inner edge of the circular muscle band. The distance from these cuticular longitudinal muscles to the outer longitudinal muscles of the parenchyma is a matter of 5 to 7 μ. In the scolex the cuticular muscles become specialized as has already been described in the preceding paragraphs. Several sets of muscles comprise the group of parenchymal muscles, the inner longitudinal muscle mass being by far the most conspicuous. It is more median than any of the other muscle systems and extends posteriorly from the scolex. It forms a ring about the vitellaria and testes and this continues with little break except for the region of the cirrus sac where the continuity is lost ventrally. A few fibers leave the inner longitudinal mass and become associated with the circular fibers surrounding the cirrus sac. The muscular ring lies 0.60 to 0.13 mm. from the surface of the parasite in the neck region. However, as it passes posteriorly the inner longitudinal muscles come to lie closer to the surface. In the anterior third they are from 0.06 to 0.096 mm. from the surface, and in the region of the vas deferens it is only 0.024 to 0.072 mm. In the portion of the parasite in which the female

reproductive system lies the musculature is found to again become more median, and the muscles are from 0.048 to 0.12 mm. from the surface. In every case the distance laterally from the inner longitudinal muscles varied but slightly over the entire length of the parasite. On the other hand the dorso-ventral aspects varied between 0.028 and 0.132 mm. Doubtless even greater differences would be noted in the cases of specimens whose uteri were filled with embryos, for the distended uterus would force the muscles towards the surface. The outer longitudinal muscle mass shows more distinctly in the posterior neck region than at any other place. This layer is indistinct and lies much closer to the basement membrane than has been noted in other species of this group. The individual muscles are grouped together 3 to 5 in a fasciculus. These occur only in the region of the neck; they disappear shortly after the vitellaria commence. Anteriorly they extend well into the scolex and become inserted, as already described, on the posterior portion of the acetabular suckers. This reminds one of the condition found in *H. paratarius* and *G. laruei.* Both dorso-ventral and lateral muscle fibers show insertions in the region of the basement membrane. These are more generally spoken of as frontal (horizontal or lateral) and sagittal (dorso-ventral) fibers. The dorso-ventral muscles are slightly more numerous than those of the lateral system. These fibers appear singly and are not connected with those of the inner longitudinal system as in the case of *Capingens singularis.* Certain organs of the parasite possess highly specialized muscles, but these will be considered in the paragraphs dealing with the organ and will not be discussed in this section.

The excretory system of this parasite has certain unique peculiarities. In the first place there is no definite number of main excretory canals, for 8, 10 or 12 may be counted according to the region examined. Anteriorly the number is reduced from 10 pairs to only 8, the former being the number found in the middle of the body, while near the posterior extremity, just before passing into the excretory bladder 12 are found. In the scolex the lateral canals extend along the base of the acetabular-like sucker. These probably aid in carrying off the wastes from this field of activity, and also in the extension of the scolex. At the base of the scolex several of the canals intercommunicate and form a plexus which may aid in the extension of this organ. The fluids pass into the plexus and then out into the canals in the scolex, thus giving it turgidity and also an opportunity to carry off wastes and carry food to the cells of this locality.

The canals of this system are paired and are composed of the typical ascending and descending canals. The former lie medianly as in *M. ingens* and are usually smaller. They begin in the region of the female reproductive system, run forward and finally in the scolex or neck pass over through small canaliculi into the channels of the descending system. The

descending canals empty into the terminal excretory bladder which is approximately 0.09 mm. in length and 0.024 to 0.036 mm. in width. This bladder lies in the horizontal plane to the left of the median line from which it abruptly turns and empties to the exterior near the ventral posterior tip of the body. The terminal excretory tube is 24 μ long and empties into an atrium 48 μ in diameter; the atrium lies to the left of the mid line. The tube itself is lined with cuticula and the cavity is 19 μ in diameter. It passes to the surface to the left of the center of the body.

The nervous system is very indistinct; two main trunks and two ganglia are visible in the neck region (Fig. 12).

The male reproductive system is composed of organs typical of the Caryophyllaeinae. The testes in this species are much more numerous than in any other species of Cestodaria studied. There are between 420 and 440 testes in the adult. This great number found in forms which reach a maximum length of 16 to 18 mm. is explained by the relatively small size of the testes and the corrallary that 5 to 6 of these may be seen in transections. The arrangement of these glands is rather similar to that noted in other species, especially *M. ingens*. There are dorsal and ventral rows of testes which each contain 3 to 4 testes. The more typical arrangement, however, is an alternation which makes for compactness. Occasionally several of the testes of this species are found connected with each other, reminding one of the possibility of a common origin for several testes. This condition, however, is unusual. An examination of 50 testes from several specimens furnish the following data:

length.............	0.084–0.168 mm.
width.............	0.049–0.120 mm.
depth.............	0.069–0.096 mm.

In making measurements the length was the distance in an anterior-posterior direction and the width was the measurement laterally, while the depth was the distance in the dorso-ventral plane (Fig. 70). The vas deferens is found in the middle portion of the medullary parenchyma. It assumes a somewhat zig-zag course posteriorly, tapping the various testes and groups of testes until the region just anterior to the seminal vesicle is reached. Here the testes and vitellaria disappear from the center of the field and the vas deferens fills the entire area except for the extreme lateral portions of the medullary parenchyma which is still filled with testicular and vitellarian follicles. The vas deferens increases rapidly in size, and becomes distended with spermatozoa. The diameter, for example, of the non-distended portions is from 0.036 to 0.052 mm.; this now increases from 0.108 to 0.156 mm. in greatest diameter. In this species the expanded part of the vas deferens is more sac like than tubular, for these large cavities are free and interconnecting. Some of these long loose

convolutions extend posteriorly for 0.18 to 0.2 mm. before they recurve. As the vas deferens begins to increase in size it passes dorsally and after several convolutions crowds out the ventral testes and vitellaria and gradually assumes a rough triangular shape with the base of the triangle on the cirrus sac.

The uterus in this form, like *H. paratarius*, extends anteriorly beyond the cirrus sac. Thus the coils of the uterus begin to crowd the vas deferens ventrally and this process continues until the vas deferens is forced to the right side where it supplants the testes and vitellaria. The latter still persist near the left margin. The convolutions of the vas deferens appear earlier than the eggs in the uterus. In *H. paratarius* only a few eggs were found and yet a similar distended vas deferens was characteristic. In this species a similar situation prevails, except that no eggs appear in the uterus. The vas deferens reaches a position which is midway between the dorsal and ventral surfaces and to the right of the middle of the body. Here it forms a characteristic muscular ductus ejaculatorius which has a diameter of 16 μ the walls being 4 to 5.3 μ thick and the cavity 6 to 7 μ. This tube passes into the seminal vesicle which lies in the ventral half of the parasite, anterior to the cirrus sac. The tube enters the right dorsal surface of the seminal vesicle. This structure slopes slightly ventrally and the long axis is towards the center of the parasite (Figs. 32, 48). This vesicle differs from all of the others which have heretofore come under my observation in that the circular muscles surrounding the cavity of the vesicle are in turn enveloped by a layer of cells. This cellular layer is 10 to 18 μ thick and is composed of cells in which the cytoplasm takes little or no eosin. The nucleus stains deeply with hematoxylin and the nucleoplasm is deeply pigmented. Two deep blue nucleoli appear in the more central portion of the nucleus. From the nucleus radial thread-like structures extend across the cytoplasm to the cell wall (Fig. 69). This cellular layer shows to best advantage in a sagittal section where the cells stand out with great clearness. Under this lie the circular muscles from 5.3 to 6.3 μ thick, while the lining of the cavity is slightly less than 1 μ. The cavity has a minimum length of 70 μ and a maximum length of 135 μ; the extended condition is more typical. The cavity is usually round and has a diameter of 48 to 50 μ, although it may become as narrow as 24 by 48 μ. Such variations are due to differences in contraction not only of the specimen but also of the vesicle.

The remainder of the ductus ejaculatorius is short; it leaves the seminal vesicle at its posterior end and passes dorsally past the side of the cirrus sac to a position above and more median than the seminal vesicle. The tube is from 24 to 30 μ in total diameter and enters the cirrus sac on the anterior dorsal surface (Fig. 18). The duct is surrounded by a thin layer of circular muscles. The cells peculiar to the seminal vesicle are also present in small numbers about the muscle layer of the ductus ejaculatorius.

The cirrus sac is nearly round and has a maximum diameter of 0.144 mm. The sac is not highly muscular for the layer of circular muscles surrounding the sac are only 19 to 24 μ in thickness. The measurements of the cirrus sac in both cross and sagittal sections give a maximum width of 0.18 mm. and a length (anterior-posteriorly) of 0.225 mm. (Fig. 48). If the cirrus is extruded the cirrus sac assumes a more pyriform shape. In such cases the retractile fibers may be clearly seen extending from the apex of the cirrus and the base of it to the walls of the cirrus sac opposite the point of exit of the cirrus. Measurements of the extruded cirrus in three specimens gave the following data:

length of cirrus extruded	0.168–0.192 mm.
diameter of cirrus at apex	0.055–0.065
diameter of cirrus in middle	0.067–0.072
diameter of cirrus at base	0.069–0.074
diameter of urethra	0.019–0.024

The musculature of the cirrus showed to good advantage in the sagittal sections. In one specimen the cirrus was not fully extruded, but the arrangement of the muscles showed clearly. The contraction of the circular muscles forced the cirrus out. This was indicated by the contracted appearance of the muscles and by the fact that in an unextruded specimen the tube which pierces the cirrus is loosely coiled within the confines of the sac. Longitudinal muscle fibers extend from the distal tip of the cirrus to the median walls of the cirrus sac. Other fibers run from the base of the cirrus to the median wall of the sac. The cirrus sac is flanked laterally by the arms of the ovary which extend anteriorly beyond it. The cirrus sac and the female cloaca open into a common atrium, which is 48 to 50 μ in depth and serves as a cloaca for both the male and the female reproductive systems. The male system, however, empties from the anterior side into the utero-vaginal canal coming ventrally from a position directly dorsal (Fig. 48). In this respect the male system resembles that of the genus Caryophyllaeides, Nybelin (1922).

The ovary is lobate and assumes the "H" shape so characteristic of the Caryophyllaeinae. The commissure which connects the two main arms of the ovary is nearly circular and has a diameter of about 0.168 mm. The length of the main arms varies from 0.6 to 0.65 mm. Anteriorly they extend beyond the cirrus sac, even in relatively uncontracted specimens. The ovary fills the bulk of the medullary parenchyma and is 0.182 to 0.253 mm. in depth. The ovarian commissure lies slightly ventral to the mid line and divides the ovary into two equal parts. The commissure also serves as an ovarian reservoir. The oöcapt takes its origin from the median ventral side. It consists of a circular sphincter muscle 7 to 9 μ in thickness which guards the entrance into the oviduct and controls the release of the ova. The vagina appears in the same section above the ovarian commissure. It leaves

the female cloaca on the posterior side a little ventral to the point where the uterus empties in from above. Immediately the vagina becomes distended into a large receptaculum seminis. This measures about 0.1 mm. in length and has a maximum width of 0.048 mm. (Fig. 32). The receptaculum seminis is filled with spermatozoa. These are typically flagellate and measure 10 to 11 μ in length. The head piece is 2.1 by 0.8 to 1 μ. The vagina passes posteriorly and dorsally until it reaches a position directly above the ovarian commissure. It is at this point that the oöcapt leaves the commissure ventrally (Fig. 85). The vagina then passes ventrally, to the left and goes into the oötype along with the vitelline duct and the oviduct. The vagina is surrounded throughout most of its course by a layer of circular muscles 5 to 7 μ thick which in turn is covered with a layer of cells. The oviduct arising from the distal end of the oöcapt passes ventrally and then to the left where it is immediately joined by the vagina which has passed down from a position dorsal to the ovarian commissure. The union of these two ducts marks the formation of the fertilization chamber, or the vaginal-oviducal canal. This duct passes posteriorly for a short distance before it is joined by the unpaired vitelline duct, coming from the anterior part of the body. This passes ventrally and turns up to meet the vaginal-oviducal canal from the posterior ventral side. Thus the uterus is formed; it passes through the highly glandular oötype to the posterior regions of the body. The uterus, after leaving the oötype is thin walled, and the characteristic uterine glands only make their appearance when the most posterior part of the uterus is reached. These glands persist and are found around the convoluted uterus until it has passed the cirrus sac and reached its most anterior position and started posteriorly to empty into the female cloaca. The uterine glands are present until the last two convolutions of the uterus are reached where they gradually disappear. The vitelline ducts are paired in the anterior body parts. These canals are situated laterally to the vas deferens which runs up the center of the worm. Posterior to the region of the cirrus sac the two canals fuse and become one. The post-ovarian vitellaria lie distally to the uterus. A single duct arising medianly runs anteriorly and joins the main vitelline duct before it empties into the vaginal-oviducal canal. The eggs of this species are not present in the available material. Even though the female reproductive system is apparently fully developed no eggs are found in the distal positions of the uterus. As this material was not secured until the winter it is possible that they were taken at a season when the parasites were sexually inactive. However, it is also possible that this parasite normally would not become sexually mature until the following spring.

Biacetabulum infrequens because of its monozootic nature, coupled with the arrangement of the reproductive organs, clearly falls into the Caryophyllaeidae. The form belongs in the Caryophyllaeinae owing to the

medullary position of the inner longitudinal muscles which surround the vitellaria. It is excluded from the genera Caryophyllaeus, Monobothrium and Glaridacris by the shape of the scolex and the uterine coils which never extend anteriorly to the cirrus sac. *Biacetabulum infrequens* is also excluded from the genus Archigetes on the basis of the scolex, excretory system, host and the possession of a caudal vesicle bearing the embryonic hooks. The only other possibilities which remain lie in the genera Caryophyllaeides and Hypocaryophyllaeus. The former is barred by the specialization of the scolex, shape of the ovary, and the maximum distance the uterine coils extend in relation to the testes. It differs from the latter in the type of scolex, the longitudinal extent of the uterine coils in relation to the cirrus sac as well as the type of genital atrium. It was therefore necessary to create a new genus and species to hold this form, *Biacetabulum infrequens* Hunter (1927).

BIACETABULUM MERIDIANUM HUNTER 1929

[Figs. 15, 34, 46, 47, 64, 65, 90]

1929: *Biacetabulum meridianum* Hunter 1929: 190

Specific diagnosis: With the characters of the genus. Adult parasites 5 to 15 by 0.4 to 0.8 mm. Scolex fairly prominent and is set off from the body which is flattened dorso-ventrally by a well defined neck. Cuticula 4 to 6 μ thick; underlaid by thin subcuticula 6 to 16 μ deep followed by cortical parenchyma 50 to 70 μ thick. Cuticular, outer and inner longitudinal muscles, all present and prominent. Testes 65 to 95 roughly oval, with maximum diameter from 0.13 to 0.15 mm. Vas deferens confined medianly between uterine coils; short ductus ejaculatorius precedes "L" shaped seminal vesicle 0.13 to 0.27 mm. long, extending from the ventral to the dorsal surface of the medullary parenchyma. Cirrus sac round, occupies one-fourth to one-half of the medullary parenchyma; diameter from 0.13 to 0.2 mm.; circular muscles of this organ 10 to 15 μ thick. Male reproductive system opens into the combined utero-vaginal canal 0.04 to 0.07 mm. from the outside. Vagina median, convoluted and forms crescent shaped receptaculum seminis about 70 μ in length just before passing over ovarian commissure. Ovarian wings are 0.3 to 0.4 mm. by 0.9 to 0.15 mm. The last third of the uterus not surrounded by typical uterine glands and this portion lies anterior to ovarian commissure. Vitellaria with maximum diameter of 0.08 to 0.13 mm. Eight pairs of main excretory canals terminating in excretory vesicle 45 to 60 μ long by 20 to 25 μ wide. Eggs oviform 48 to 54 by 31 to 37 μ.

Host: *Erimyzon sucetta*, Eno River, North Carolina. In intestine.

Type: Slide in the collection of Dr. Henry B. Ward, No. 29.43

Paratypes: Slides and bottled material in author's collection, No. 687.2 –687.6.

Host	Locality	Collector	Authority
Erimyzon sucetta (Lacépède)	Eno River, Durham, N. C.	F. J. Holl	Hunter (the present paper)

The material forming the basis for the description of this species was collected by Dr. F. J. Holl while at Duke University, Durham, N. C. He examined 14 specimens of *Erimyzon sucetta* and only found three or 21.4% infected. These three according to Dr. Holl's records harbored 1, 50 and 73 Cestodaria respectively. The author examined several specimens from the vicinity of Urbana, Illinois, during 1925 and 1926 but did not find any infected with Cestodaria.

These parasites present the typically monotonous external form which is characteristic of the Caryophyllaeinae. The scolex appears slightly broader than the remainder of the body (Fig. 15). It measures 0.4 to 0.6 mm. in longitudinal extent and 0.4 to 0.55 mm. in width. The widest part is the base of the scolex, just posterior to the two main suckers which lie on the median dorsal and ventral surface. These acetabular-like suckers are 0.15 to 0.25 mm. in diameter in cross section and 0.2 to 0.27 mm. in a logitudinal plane, are rather shallow and measure 70 to 100 μ in thickness. This is the distance from the bottom of the cup to the back of the cup and is sometimes designated as base to back. The suckers are only weakly acetabular in nature and do not stand out as distinctly as those of *B. infrequens*. The outer longitudinal muscles are attached to the proximal margin of the sucker while most of the inner longitudinal fibers are dissipated on the distal margins of the cup (Figs. 64, 65). Some of these are not attached to the sucker but pass directly to the distal portion of the scolex. The acetabular nature of the scolex is brought out in figure 65 which also indicates a certain motility of the suckers. Evidently it is possible for them to create a lot of suction and no doubt are capable of some motion and rotation due to the nature of the musculature. Throughout the scolex are found a number of muscle fibers; these extend dorso-ventrally and also laterally.

Within the medullary parenchyma are found two ascending tubes of the excretory system. Before the suckers are reached these tubes pass laterally and connect with a ring which extends around the cortical parenchyma of this organ and gives off several pairs of descending canals. In the neck these tubes divide giving rise to 8 which number remains constant throughout the body. The two ascending tubes from the medullary parenchyma have now become subdivided and paired with their mates of the descending system. These pass posteriorly through the cortical parenchyma while the descend-

ing tubes empty posteriorly into the small terminal excretory vesicle. Like others this vesicle is pear-shaped and at its proximal end (which is also the widest part of the bladder) the descending canals empty; it is only 45 to 60 μ in length and 20 to 25 μ broad and is lined throughout by a continuation of the cuticula.

The neck is somewhat narrower than the body and varies from 0.3 to 0.6 mm. in length and 0.2 to 0.4 mm. in width. The musculature is clearly discernible here, even the small cuticular muscles. In this region the cortical parenchyma reaches a maximum width of 95μ and the medullary parenchyma is correspondingly reduced; no change in the thickness of the subcuticula was noted. In the body proper this layer remains very thin being only 6 to 15 μ deep. Towards the outside and embedded in this are the longitudinal and circular cuticular muscles, while the outermost limits of the subcuticula are bounded by a poorly defined basement membrane. This layer constitutes the innermost one of the cuticula which is only 4 to 6 μ thick. At the inner edge of the subcuticula lies the outer longitudinal muscles which separate this from the adjoining layer of the cortical parenchyma. These muscles contain but two or three fibers per fasciculus and these in turn are located 5 to 15 μ apart. The distance of this layer from the outside. changes but little. At the innermost margin of the cortical parenchyma lie the more prominent inner longitudinal muscles containing 6 to 10 individual fibers in each fasciculus. This layer lies between 60 and 90 μ of the outside of the parasite except in the neck and base of the scolex where the fibers are drawn closer to the center of the body and the distances reach a maximum of about 120 μ (Figs. 65, 90).

The testes number from 65 to 95, are generally ovoid in shape and possess a maximum diameter of 0.13 to 0.16 mm. In cross section there is a dorsal and ventral row bounded laterally by vitellaria. There occur two to three testes per row and as many vitellaria. As the cirrus sac is approached the testes and vitellaria in the mid regions are displaced by the invading uterine coils. Just anterior to and between these occur the thin walled twisted vas deferens. This may occupy but a small part of the medullary parenchyma even when filled with spermatozoa, as only the mid dorsal portion of the medullary parenchyma is occupied. Laterally it is surrounded by the uterine coils and the vitellaria, altho in specimens which contained empty vas deferentia the major part of this organ lay anterior to the invading uterine coils and not median to them. The coils of the vas deferens have a maximum diameter of 30 to 47 μ. The ductus ejaculatorius arises from the most median ventral coil of the vas deferens; it passes ventrally only 30 to 50 μ before expanding into the more muscular seminal vesicle. This vesicle is prominent and "L" shaped, much longer than wide, extending posteriorly and dorsally at an angle of about 30 degrees with the vertical. It turns on itself and dips towards the ventral surface, passing into another short

narrow portion of the ductus ejaculatorius before penetrating the cirrus sac (Fig. 46). The seminal vesicle is 0.13 to 0.27 mm. in length and 0.03 to 0.05 mm. in width; the layer of circular muscles varies from 6 to 9 μ in thickness. The cirrus sac is round and has a maximum diameter of 0.139 to 0.2 mm.; the circular muscles are thin being 10 to 15 μ thick. The cirrus sac is tilted at a slight angle so that the cirrus opens posteriorly into the utero-vaginal canal of the female reproductive system which in turn is even with the surface.

This canal, as the name implies, is composed of two elements, the uterus and the vagina. It extends in a dorso-ventral direction. The male reproductive system empties 0.04 to 0.07 mm. from the ventral surface. The vagina proceeds posteriorly and ventrally while the uterus comes in from an anterior dorsal position. Just prior to its union with the vagina to form the utero-vaginal canal there is a well defined sphincter muscle which regulates the discharge of the eggs (Fig. 46). The vagina continues on its ventral swing until close to the inner longitudinal muscles where it becomes somewhat straighter and continues posteriorly in a convoluted path until the ovarian commissure is reached. The receptaculum seminis is formed anterior to the ovarian commissure but level with middle of the ovarian commissure; it runs dorsally and is completed as the vagina passes over the commissure. (See Figs. 46, 47.) The cavity is 0.06 to 0.08 mm. long and 0.015 to 0.025 mm. in width. It is somewhat crescent shaped and is surrounded by a layer of circular muscles 4 μ deep. After passing the ovarian commissure the vagina dips to the left and posteriorly until nearly the end of the ovarian wing where it curls on itself and winds medianly to the spot where it joins the oviduct to form the fertilization chamber (Fig. 34). The vitellaria are present as two lateral rows joined by an intersprinkling of these glands between the testes which they tend to surround. They are joined anteriorly to the testes and the lateral vitellaria extend posteriorly to within 50 μ of the ovary (Fig. 34). Post-ovarian vitellaria are also present. The vitelline glands range in size from 0.08 to 0.13 mm. in maximum diameter which normally is found in a dorso-ventral plane. The ducts arise in the mid line just median to the two lateral rows of testes, they continue posteriorly until the ovary is reached. As usual these canals pass median to the ovarian wings and over the ovarian commissure. In doing this the vitelline ducts are lateral but on the same plane as the vagina and the uterus. Posterior to the commissure the left vitelline duct is joined by one from the post-ovarian vitellaria which followed the inner longitudinal muscles closely (Fig. 47). These united ducts pass laterally as a vitelline reservoir and are joined by the one from the right side, thus forming the common vitelline reservoir, and later duct.

The globular ovary is "H" shaped with ovarian wings varying from 0.3 to 0.4 mm. in length and 0.13 to 0.16 mm. in width. The commissure of this

gland is posterior to the center and measures 0.09 to 0.12 mm. in cross section. The oviduct arises from the ventral posterior portion of the commissure by means of a well defined oöcapt which is 20 μ in diameter. The muscles are 5 to 6 μ thick and the whole structure is funnel shaped with most of the muscles at the base of the flare of the funnel. The oviduct is only about 50 μ in length; it passes posteriorly to the left in an arc which carries it anteriorly again. It is at the outer edge of the oötype and is joined by the vagina, forming the fertilization chamber; this canal continues posteriorly describing a larger reverse arc for over 100 μ, picking up the common vitelline reservoir duct about the middle of the body and but 50 μ from the beginning of the fertilization chamber. Immediately after uniting with the vitelline duct a number of glands of the oötype are passed (Fig. 47). The uterus continues by numerous convolutions posteriorly through the oötype finally passing dorsally to form the ascending limb of the uterus proper which is surrounded by the typical uterine glands. After passing the ovarian commissure the uterus becomes highly convoluted which continues until the cirrus sac is passed. This area is filled dorsally, ventrally and latally except for a single row of vitellaria along the side. As the uterus bends posteriorly again, the uterine glands begin to disappear, so that most of one loop from the cirrus sac to the ovarian commissure and back (until anterior to the cirrus sac again) is composed of a uterine tube devoid of the typical uterine glands. Instead is a layer of circular muscles which are 2 to 3 μ in thickness. Approximately one third of the uterus is so lined. Just before the uterus joins the vagina there is the uterine sphincter which has previously been described (Figs. 34, 46). The eggs are oviform and measure 48 to 54μ by 31 to 37μ.

This parasite clearly belongs in the genus Biacetabulum on the basis of the scolex, acetabular sucker and type of genital atrium. *Biacetabulum meridianum* differs from the type species, *B. infrequens*, in the development of the one pair of acetabular suckers, which are more highly specialized in the case of the type species. It is natural that the arrangement of the reproductive systems should have much in common; the testes, however, number 65 to 95 in *B. meridianum* compared with 420 to 440 in *B. infrequens*. Likewise the vitellaria are typically smaller in the type species altho the maximum diameters are essentially the same (Fig. 90). The seminal vesicle is much larger and longer in *B. meridianum* than in *B. infrequens* measuring 0.13 to 0.27 mm. compared with a maximum of 0.107 mm. for the latter species. Furthermore the layer of deep staining cells so characteristic of the type species is absent from *B. meridianum* and the receptaculum seminis is consistently smaller in the latter species and is located closer to the ovarian commissure. The excretory vesicle is smaller and the 6 pairs of excretory canals remain unchanged in *B. meridianum*. Other important differences which should be stressed are (1) the thickness of the cirrus sac muscles,

which is greater in *B. meridianum*, (2) the position of the vas deferens here confined to the region between the coils of the uterus while in the type species it is found at one side, (3) the uterine coils, which are without the characteristic uterine glands, are confined to regions anterior to the cirrus sac in *B. infrequens* while in *B. meridianum* they extend to the ovarian commissure and back in addition, (4) the well defined sphincter muscle of *B. meridianum* and (5) the hosts of the two parasites are different. This brief summary constitutes the main points of difference between these forms. This new species herein described was named *Biacetabulum meridianum* to denote the locality from whence it came.

BIACETABULUM GIGANTEUM HUNTER 1929

[Figs. 18, 33, 40, 53–60]

1929: *Biacetabulum giganteum* Hunter 1929: 190–191

Specific diagnosis: With the characters of the genus. Adults 7 to 16 mm. by 0.8 to 1.08 mm.; posterior half of body flattened dorso-ventrally. Scolex resembling the well developed "II" type, bearing four loculi, and two median well developed acetabular-like suckers. Cuticula 7 to 9 μ thick; subcuticula and cortical parenchyma reduced to a minimum in the posterior half of the body, together are 0.038 to 0.070 mm. thick. Medullary parenchyma occupies three fourths to seven eighths of body width. Inner longitudinal musculature reduced to eight fasciculi in the base of the scolex; outer longitudinal muscles prominent throughout the body as are the cuticular muscles. Testes irregularly oval, 0.12 to 0.2 mm. in greatest diameter and number 165 to 215. Vas deferens may fill entire medullary parenchyma; seminal vesicle 0.13 to 0.2 mm. by 0.08 to 0.12 mm. Ductus ejaculatorius straight, about 0.15 mm. long. Cirrus sac ovoid, 0.22 to 0.27 mm. in diameter; the muscles are 33 to 47 μ thick. Cirrus opens into utero-vaginal canal. Vagina ventral, straight, thick-walled and forms a receptaculum seminis 0.060 to 0.142 mm. by 0.035 to 0.06 mm. Ovarian wings 0.37 to 0.54 mm. by 0.16 to 0.23 mm. Vitellaria surround the testes and are 0.13 to 0.23 mm. in maximum diameter. Excretory system has 8 pairs of canals; the descending canals empty into an excretory vesicle 40 to 60 μ long by 18 to 25 μ in width.

Host: *Ictiobus bubalus* and Ictiobus sp., Tallahatchie River, Mississippi. In intestine.

Type: Slides of author's material in the collection of Dr. Henry B. Ward, No. 29.44.

Paratypes: Slides in the collection of the Department of Zoology, University of Minnesota. Slides and vials Nos. 628, 651.2, also 653, 655, and 659 in author's collection.

Host	Locality	Collector	Authority
Ictiobus sp.	Tallahatchie River, Money, Miss.	Parke H. Simer	Hunter (the present paper)
Ictiobus bubalus (Rafinesque)	Tallahatchie River, Money, Miss.	Parke H. Simer	Hunter (the present paper)
Ictiobus bubalus (Rafinesque)	Mississippi River Fairport, Ia.	——	Hunter (the present paper)
Ictiobus cyprinella (Cuv. and Valenciennes)	Rock River, Sterling, Ill.	J. F. Müller	Hunter (the present paper)
Ictiobus cyprinella (Cuv. and Valenciennes)	Mississippi River, Lake Pepin, Minn.	G. W. Hunter, III and H. E. Essex	Hunter (the present paper)

This species was found in the Mississippi collection of Dr. Parke H. Simer. The parasites were of moderate size, 7 to 16 mm. in length by 0.8 to 1.08 mm. in breadth, while the body was divisible into a well defined scolex, neck and body. The scolex resembled the Glaridacris "II" type and is 0.67 to 1.0 mm. long by 0.67 to 1.3 mm. wide. Of the six organs of adhesion which were visible the median acetabular ones appeared to be the most efficacious. These were oval and resembled suckers in totos; they measured 0.4 to 0.5 mm. long and 0.27 to 0.3 mm. wide (Fig. 18). At the base of the scolex the diameter becomes highly reduced as it passes into the narrow neck. The scolex is filled with bundles of muscles, some inserted on its flat distal portion. One tenth mm. from the tip the number of fibers is increased and the mid region is dotted with a mass of individual fibers. (These are represented slightly out of proportion in Figs. 54-60.) As the loculi are reached the scolex becomes cut by these and in each projecting ridge of tissue between them is a bundle of muscles traceable to the inner longitudinal system. Through this region are also found numerous transverse and dorso-ventral cuticular muscles (Figs. 56–58). The two median depressions resemble true suckers more closely than the other four, and these are not only deeper, but much larger. As in *B. infrequens* the cuticular muscles connect the base of the suckers back to back; nuclei are also found concentrated in this area (Figs. 56–58). As the lower end of the scolex is approached the muscles are drawn together and concentrated into eight fasciculi, four in each lateral third of the scolex as in *G. confusus* (Figs.

57–60). The base of the scolex (Fig. 60) shows the fasciculi more equally scattered and as the neck is reached these become more concentrated until practically the entire medullary parenchyma is filled. Canals of the excretory system are present from the region of the loculi posteriorly and are very prominent in the neck.

The neck is rather long and narrow being 1.2 to 2.6 mm. in length and having a maximum width of 0.3 to 0.47 mm. The middle region is filled with muscles which posteriorly become pushed aside, the space becoming filled with the reproductive organs. The cuticula is well defined and 7 to 9μ thick. This layer takes the stain quite evenly throughout. Beneath it lie the cuticular muscles, the circular and longitudinal muscles having a combined thickness of 4 to 5 μ. These are situated in the subcuticular layer of the parenchyma which varies between 8 and 20 μ in depth; it is usually about 10 μ except in the neck where it becomes thicker. At the inner edge of this layer is a well defined set of outer longitudinal muscles which are 5 to 7 μ thick and consist of three to five muscle fibers per fasciculus. The cortical parenchyma is bounded medianly by the inner longitudinal muscles; it is 30 to 50 μ thick and in the neck is sometimes 75 μ deep. The inner longitudinal musculature is by far the most conspicuous muscle layer and is normally 10 to 15 μ in thickness, but reaches a maximum of 60 μ in the neck. In this region it fills the entire parenchymal field.

The excretory system is remarkably clear in this form and will consequently be described at some length. The canals are paired, there being 8 pairs of main canals in all of the specimens examined. The inner one is slightly smaller and has a thicker wall. At the beginning of the neck the 8 pairs of inner canals fuse to form 4 and each pair invades the medullary parenchyma of the neck. These in turn are reduced to 2 pairs as the base of the scolex is approached. They preserve their integrity until the anterior part of the scolex is reached where the internal pair fuses with its companionate descending tubule. The shape of this scolex must remain relatively unchanged since there are so few excretory canals in this region. These outer tubules pass back through the scolex (as previously noted) divide in the neck, pass to the cortical parenchyma and proceed posteriorly to the excretory bladder. This vesicle 40 to 60 μ long and 18 to 25 μ wide, in cross section is serrate; the reduced cuticula extends inwards as the lining of this cavity. There are of course a number of smaller intercommunicating canals, but it is impossible to trace these out in preserved material.

The testes numbering 165 to 215 are irregularly spherical to ovoid in shape and measure 0.16 to 0.2 mm. in maximum diameter. In the last third of the testicular field the vas deferens becomes noticeable. This assumes a central position while the two vitelline ducts are located more laterally; they lie just median to the lateral rows of the vitellaria (Fig. 53). In cross section there are usually two to three testes in the dorsal and ventral rows although

this number may be augmented occasionally. As the posterior limits of the testicular field are passed the vas deferens expands and frequently fills the entire medullary parenchyma at least in a dorso-ventral plane; the maximum diameter varies between 0.1 and 0.21 mm. (Fig. 33). However this does not occur in specimens in which the vas deferens is not swollen with spermatozoa. It gradually narrows down to pass into the seminal vesicle which is 0.13 to 0.2 mm. in length. In spite of its central appearance in figure 33 it is more normally found to the left of the cirrus sac. The main axis of the seminal vesicle is in a dorso-ventral plane and is surrounded by a layer of circular muscles 15 to 26 μ wide while the cavity is 0.1 to 0.2 mm. long by 0.06 to 0.1 mm. wide; it is penetrated from the dorsal surface and passes ventrally into a short straight ductus ejaculatorius which is about 0.16 mm. long and penetrates the cirrus sac from the median anterior surface. The muscles which line the vessel are 7 to 9 μ thick and the tube itself is 15 μ wide making a total diameter of about 30 μ. The cirrus sac is fairly small having a diameter of 0.2 to 0.27 mm. and a heavy layer of muscles which varies between 33 and 47 μ. The general shape is round and there are nuclei found occasionally scattered through the muscles as well as within and without the layer. The extended cirrus is 0.13 to 0.2 mm. in length and about 0.033 mm. in breadth. The cirrus sac opens into the utero-vaginal canal (Fig. 40).

The utero-vaginal canal extends dorsally for about 0.1 mm. before it gives off the vagina which leaves and remains close to the median ventral surface of the medullary parenchyma. It is relatively straight, and is only 7 to 8 μ wide and thin walled. As it approaches the ovarian commissure it crosses to the right and passes over the middle of the commissure and in so doing forms a receptaculum seminis. This structure is lined by a cuticula-like substance, followed by 2 to 4 μ of circular muscles which in turn are bounded by a cellular layer 5 to 15 μ in thickness. The receptaculum seminis varies from 0.06 to 0.125 mm. in length and 0.035 to 0.05 mm. in width; it passes over the vitelline ducts and dips ventrally into the oötype complex where it joins the oviduct 60 to 80 μ from its point of origin. The vitellaria surround the testes and are from 0.13 to 0.23 mm. in maximum diameter. The vitelline ducts descend in the usual manner, meet just dorsal to the ovarian commissure, and pick up a duct from the right margin of the post-ovarian vitellaria (cf. *G. confusus*). The ovary is 0.37 to 0.54 mm. by 0.16 to 0.23 mm. It is globular in contrast with *G. confusus* and is quite small compared with many species, even in well expanded specimens (Fig. 33). The ovarian wings are so broad that the commissure is quite short and has a maximum diameter of 0.14 mm. The oviduct arises from the middle of the ovarian commissure about mid way between the dorsal and ventral surfaces. It arises through a small oöcapt, passes posteriorly for 20 to 30 μ, turns up for 40 to 50 μ and unites with the vagina at the peak of the arc.

The two form the fertilization chamber. This continues posteriorly through the oötype for about 25 μ before uniting with the common vitelline duct. After a number of convolutions in the oötype the uterus emerges close to the anterior edge of the post-ovarian vitellaria, becomes surrounded by the typical uterine glands, dips dorsally and then proceeds anteriorly keeping to the right of the center as in *H. paratarius*. These uterine coils extend anteriorly to the right side of the cirrus sac and then drop back to position a dorsal to the cirrus sac where it crosses to the left side, and extends anteriorly to the vas deferens before winding posteriorly to its point of exit. It crosses under the vagina to the right side, comes back to the median line and dips ventrally where it picks up the vagina one half the way down to the outside. No eggs were found in the uterus. The forms examined showed all signs of sexual maturity except the presence of eggs. In fact small particles of vitelline material were found in sections of the uterus which pointed to the probable extrusion of the ova at sometime in the not very distant past.

Biacetabulum giganteum is placed in this genus on the basis of the type of scolex; the uterine coils, which extend anteriorly to the cirrus sac and the manner in which the male reproductive system opens into the utero-vaginal canal. It resembles the type species in the general way the reproductive system is formed, but differs in several important features; the type and shape of the scolex which bears six distinct indentations in this new species; the greater thickness of the cuticula; the size and number of the testes, the size, shape and musculature of the cirrus sac; the shortness of the ovarian wings in *B. giganteum*, the comparative narrowness of the ovarian commissure; the excretory system which has a definite number of tubules (8), and the excretory bladder which is larger in the type species; and finally the hosts themselves.

Biacetabulum giganteum differs from *B. meridianum* in the following respects: the scolex is larger and resembles the "Π" type; the cuticula is thicker, being 7 to 9 μ compared with 4 to 6 μ; the testes number 165-215 to 65–95 for *B. meridianum*; the cirrus sac and its muscles measure respectively 0.22 to 0.27 mm. and 33 to 47 μ compared with 0.13 to 0.2 mm. and 10 to 13 μ and finally both the size of the vitellaria and the host differ greatly. *Biacetabulum giganteum* was so named because of the proportionately large size of its scolex and other organs.

GENUS HYPOCARYOPHYLLAEUS HUNTER 1927

Generic diagnosis: Caryophyllaeinae with three pairs of loculi on a poorly defined scolex. Cirrus opens on ventral surface or into a shallow non-eversible genital atrium. Ovary "H" shaped and entirely medullary. Uterine coils extend anteriorly to cirrus sac, reaching a maximum longitudinal extent of one-fourth or less that of the testicular field. Terminal ex-

cretory bladder and external seminal vesicle present. Post-ovarian vitellaria present. Parasitic in the intestine of Catostomidae. Development unknown.

Type species: *Hypocaryophyllaeus paratarius*. Hunter 1927.

To include: *Hypocaryophyllaeus paratarius* Hunter 1927.

The members of this genus are confined exclusively to fish of two genera of the Catostomidae, Carpiodes and Ictiobus. Both genera are fairly closely alike in feeding habits and in natural habitat. When these fish were seined we often secured both genera in the same haul. This was done time and again along the Mississippi River. The type species was found only in fish from the Rock River in Illinois and the Mississippi River near Fairport, Iowa. The genus was named Hypocaryophyllaeus because of the small size of the type species.

HYPOCARYOPHYLLAEUS PARATARIUS HUNTER 1927

[Figs. 5–7, 27, 37, 38]

1927: *Hypocaryophyllaeus paratarius* Hunter 1927: 22–23

Specific diagnosis: With the characters of the genus. Adults 7 to 10 mm. by 0.15 to 0.3 mm., flattened dorso-ventrally. Scolex bears 6 weak loculi and is roughly wedge shaped. Cuticula is 3 to 6 μ thick, and the subcuticula and cortical parenchyma have a combined width of 30 to 73 μ. The latter figure is more typical of the adults. Medullary parenchyma occupies about one-half of the body width. Inner longitudinal muscles reduced to 8 fasciculi in the neck. Outer longitudinal muscles only found in the neck and soon disappear. Testes number 60 to 85 and are very small measuring 80 to 100 μ by 43 to 55 μ. Cirrus sac occupies two-thirds of the medullary parenchyma with maximum diameter of 0.105 mm., the circular muscles of 12 to 15 μ. Male and female reproductive systems open on the surface 50 μ apart. Vagina straight and forms a distinct receptaculum seminis 0.125 to 0.135 mm. in length, very thick walled, being surrounded with circular muscles of the same thickness as those found about the cirrus sac proper. Vitellaria surround the testes with maximum diameter of 52 to 73 μ. Six pairs of main excretory canals. Eggs of this species small, ovoid, non-operculate, 26 to 32 by 18 to 21 μ.

Host: *Carpiodes carpio*, *Carpiodes velifer* and *Ictiobus cyprinella*, from the Rock and Mississippi rivers, Illinois and Iowa. In intestine.

Type: Slides No. 29.45 a-b in the collection of Dr. Henry B. Ward.

Paratypes: Slides in the collection of the Department of Zoology, University of Minnesota. Slides and vials No. 274, 304.2–304.3 in the collection of the author.

Host	Locality	Collector	Authority
Carpiodes carpio (Rafinesque)	Rock River, Sterling, Illinois Mississippi River, Ia.	J. F. Müller G. W. Hunter, III	Hunter (the present paper)
Carpiodes velifer (Rafinesque)	Rock River, Sterling, Ill.	J. F. Müller	Hunter (the present paper)
Ictiobus cyprinella (Cuv. and Valenciennes)	Mississippi River, Fairport, Ia.	G. W. Hunter, III	Hunter (the present paper)

The material furnishing the basis for the description of this species was secured from members of the family Catostomidae, the genera Carpiodes and Ictiobus. The bulk of the parasites were found in the upper half of the intestinal tract of *Carpiodes carpio*. Most of the fish came from the Rock River, although some of the material came from the Mississippi River.

Hypocaryophyllaeus paratarius is characterized by a rather long thin body which tapers posteriorly to a distinct apex. The length of the adult specimens varies from 7 to 10 mm. in length and 0.15 to 0.3 mm. in breadth. The average width based upon the measurements of 14 adults is 0.215 mm. The scolex is a poorly defined structure, capable of considerable variation in shape and size due to the extreme development of the longitudinal muscles which extend to its anterior extremity; in life there is considerable variation in the size and shape of the scolex due to the contraction of the aforementioned muscles. In preserved material, as in life, the scolex is wider than the remainder of the body and measures 0.25 to 0.28 mm. in length and 0.3 to 0.56 in width and bears upon the dorsal and ventral surface three pairs of ill-defined loculi (Fig. 5). Of these six loculi the central one is the most efficacious. Even in the contracted specimens the suckers are shallow and are not provided with hooks of any sort.

Hypocaryophyllaeus paratarius is further characterized by an unusually large amount of subcuticular and cortical tissue. This species is unique, for this layer constitutes nearly one-half the width of the parasite. It confines the reproductive organs to unusually narrow limits. One specimen, for example, gave the following data, the cuticula and subcuticula measured 0.055 mm. while the total width of the parasite was only 0.22 mm. This case clearly shows that the vitellaria and testes are confined to a region nearly one half the width of the worm. Such a condition is characteristic for the species. The testes lie in two irregular rows and are surrounded

laterally by the vitellaria, which in turn are surrounded by the inner longitudinal muscles. By actual count there are between 60 and 85 testes in the sexually mature adults. The testes of several parasites ranged from 88 to 100 μ in length and 52 to 55 μ in width. The vitellaria of the adults show variation in size; measurements give a length of 52 to 73 μ and a width of 24 to 38 μ. Post-ovarian vitellaria are present. The female reproductive system is confined to the posterior fifth of the body. This character is specific for *H. paratarius*.

The scolex is broader than the body and has an indefinite shape (Fig. 5). In cross section the six loculi appear, although they are universally weak (Fig. 27). Differences in degree of contraction do not alter the shape in cross section which tapers anteriorly to a rather blunt wedge shaped tip (Fig. 6). The inner longitudinal muscle band is heavy many of the fibers extending to the lateral portions of the scolex where they become lost in the region of the loculi; some simply go into the wall of the scolex and are embedded in the basement membrane (Fig. 6).

The cuticula of this species is moderately thin, varying between 3 and 6 μ; it is somewhat thinner in the scolex. In young specimens the cuticula is thicker than in the adults and measures 4 to 5 μ. The average width of the cuticula based upon data from 12 specimens, young and adults, was 4.3 μ. The cuticula is composed of an outer layer which does not stain readily and an inner basement membrane which is about one-third of the total width. As in some of the other closely related forms the cuticula and cortical parenchyma cannot be readily separated. The medullary parenchyma is marked off by the type of cells and the presence of the inner longitudinal muscles. Since it is nearly impossible to separate the subcuticula and the cortical parenchyma it will be considered as a single layer. This varies from 30 to 77 μ in thickness. The narrowest width occurred in a young specimen measuring less than 1.5 mm. in length and the maximum was found in the adults. If only the adults were considered the limits of variation are 61 to 77 μ. Beneath the basement membrane of the cuticula lie the circular cuticular muscles followed by those of the longitudinal system. At intervals of 20 to 30 μ are found small ducts perforating the cuticula. These come from large glandular like cells lying just median to the longitudinal muscles and probably either function in the secretion of the cuticula-forming substance or are concerned with nourishment. The former hypothesis seems more reasonable since these cells are not connected with the organs within the medullary parenchyma. Between the longitudinal cuticular muscles and the inner longitudinal muscles are found the canals of the excretory system. Both the ascending and descending ducts penetrate this tissue. Also numerous dorso-ventral and lateral muscle fibers are present. The inner longitudinal muscles, by far the most prominent muscle system in the body, surround the vitellaria which in turn are arranged an-

nularly about the testes. This runs from the anterior tip of the scolex to the posterior portion of the body. The continuity of these muscle bundles is threatened posteriorly as the last fifth of the body is reached and is finally broken when the muscle bands along the ventral side give way to the cirrus sac of the male reproductive system. The longitudinal musculature forms a ring in the posterior portion of the body within which lie the reproductive organs. This muscle system lies at the inner edge of the cortical parenchyma and separates it from the medullary parenchyma. As the neck region is approached the individual muscle bundles are gradually drawn together into eight large fasciculi, so that the muscles pass to the scolex in four lateral (two at each end), two dorsal and two ventral bundles. The bundles are soon broken up and their contents dissipated to the apex of the scolex while a few strands disappear into the inner surface of the loculi and the basement membrane of other portions of the scolex (Fig. 27). There are dorso-ventral muscles but these appear to have their origin in isolated cells and are found scattered throughout the parenchyma of the body. A few lateral muscle fibers are also found. Two other muscle layers should be noted, a small layer of longitudinal muscles and outside of that a circular muscle layer with a thickness of 0.9 to 1.0 μ, lying beneath the basement membrane. These form the musculature of the cuticula and are known as the cuticular system. The most highly specialized musculature is found in the cirrus sac and the muscular seminal vesicle. The latter is in reality a muscular sac which possesses the ability of rapid and spasmodic contraction thereby acting as a pump and forcing the spermatozoa which are stored in the vas deferens, out through the cirrus. The muscles which surround the cirrus sac are of the same type as those about the seminal vesicle. Upon the contraction of these circular muscles the cirrus is extruded. Thus there are two sets of highly specialized circular muscles, the ones about the seminal vesicle forcing the spermatozoa out through the ductus ejaculatorius and the cirrus which has already been extended through the action of the cirrus sac musculature. A third specialized muscle is the small sphincter of the oöcapt less than 1 μ in diameter, which regulates the discharge of ova from the ovarian commissure.

The excretory system is composed of 6 pairs of main longitudinal canals which run the length of the body. In the adult specimens the walls of the system measure 1.5 μ to 1.7 μ and the total diameter is between 11 and 12 μ. These are connected by numerous passages the diameters of which are slightly less than those of the main canals. From these cross ducts extend minute canaliculi each of which eventually subdivides until a small excretory cell is reached. Anteriorly in the scolex the excretory canals break down into innumerable smaller canals, and these penetrate the base of the scolex. Posteriorly the 6 descending canals join to form a single short

excretory duct which terminates in a poorly defined excretory vesicle. This varies between 37 to 45 μ; the pore has a diameter of 2 μ.

The nervous system shows indistinctly, even in the material which was stained with iron hematoxylin. The system is composed of two main nerve trunks. These extend posteriorly from the base of the scolex where the two ganglia are joined by commissures. The nerve strands give off several large branches to the inner longitudinal muscles. The nerves can be traced posteriorly only as far as the beginning of the testes. Shortly thereafter the strands seem to break up into plexuses as in the case of *Glaridacris catostomi* Cooper (1920).

The testes lie in a double row within the inner longitudinal muscle bands. The counts show that the testes number between 60 and 85, the usual count being about 74 to 76. These are surrounded by the vitellaria and the latter by the longitudinal muscle bands. The testes do not extend as far anteriorly as do the vitellaria. Measurements of the young specimens (1.5 to 2.5 mm. in length) show that the testes do not begin until the middle of the body. In adults 25 of the oval testes measures from 80 μ to 100 μ in length and 43 to 55 μ in width (Fig. 38). These seem to be contiguous medianly with the curves and twistings of the vas deferens. In other words, the vasa efferentia are so reduced in length, if they are present at all, as to be negligible. The vas deferens curves in a zig-zag fashion from one testicle to the other, the median posterior border of the testes being connected with the walls of the vas deferens. This vessel runs near the median line between the testes, and leaving them passes into the parenchymatous region which lies between these organs and the cirrus sac. This region is primarily occupied by the convolutions of the thin walled vas deferens, but in it are also found several loops of the uterus. The vas deferens leaves the testicular field medianly and immediately the walls become swollen. A close examination shows this canal to be filled with minute spermatozoa. This duct passes dorsally and posteriorly making three convolutions, then passes ventrally and approaches the longitudinal muscle layer. The coils of the thin walled vas deferens pass posteriorly and ventrally to the muscular seminal vesicle. The wall of the vas deferens varies from 1 to 1.5 μ while the diameter of the spermatozoan-filled posterior portion of the vas deferens is from 19 to 43 μ. As the vas deferens passes under the seminal vesicle the thin walled surface gives way to a much thicker, narrower tube. This tube, the ductus ejaculatorius, has a diameter of 11.5 μ and the walls are 3 μ thick, which means a tubular width of only 5.5 μ. It passes dorsally and enters the muscular seminal vesicle anteriorly at its ventral surface (Fig. 38). In sagittal section the seminal vesicle measures 98 by 84 μ and is surrounded by a layer of circular muscles. Within the muscular coat lies a cavity or reservoir 50 by 28μ in length, lined with tissue having a thickness of 3 μ. At the posterior end of the cavity

lies the remainder of the ductus ejaculatorius extending ventrally into the cirrus sac. This is 48 μ in length and 7 to 8 μ in width. The lining of the duct is 2μ thick and is of the same character as that which lines the seminal vesicle. The cirrus sac is a prominent organ found near the ventral surface of the parasite in the posterior region of the body. The sac is 105 μ in diameter and is surrounded by circular muscles which, when contracted, extend the muscular cirrus. The circular muscles which comprise the outer layer of the cirrus sac vary between 12 and 15 μ in thickness. The muscle mass is thickest on the ventral surface (Fig. 38). Here the muscles are essential to retain the shape of the groove through which the cirrus is extruded when the remainder of the circular muscles contract. The cirrus is 12 μ in diameter. The lining of this organ appears as a continuation of the cuticula and is 3.1 μ in thickness. The cirrus sac opens into a very shallow atrium of its own approximately 50 μ anterior to the female genital atrium.

The ovaries are situated laterally and in the rough assume the characteristic "H" shape. Those of the younger specimens resemble a bunch of grapes, and are globular. Later in adult life the contour of the individual units of the ovary is lost and only the general "H" shape remains (Fig. 37). The cross arms of the "H" forms the ovarian commissure. The ovaries from 0.1 to 0.2 mm. in length and 0.067 to 0.1 mm. in width. The oöcapt arises from this and runs ventrally. It is less than 10 μ long, is composed of weak circular muscles and gives rise to the oviduct into which empties the vagina through a small opening which is guarded by a small sphincter muscle. The opening within the limits of the muscle has a diameter of less than 1 μ in both the oöcapt and vaginal sphincters. This cavity is large enough to permit the passage of ova when the circular muscles are not contracted (Fig. 38). The ova at this point have a diameter of about 7 μ. The vagina broadens out and passes dorsally into the receptaculum seminis. This structure is not highly specialized and is not therefore readily distinguishable from the vagina proper. The tissue lining the vagina increases from 2 to 3 μ in thickness which may be accounted for by the presence of an additional layer of glandular like cells. These cells contain globules which resemble vitelline material. This receptaculum seminis has a length of 125 to 135 μ. After leaving this specialized portion of the vagina the walls again thin out to 2 μ and the surrounding cellular layer is lost. After a series of convolutions the main descending limb of the uterus is joined from the side and the vagina and uterus empty by a common duct, the cloaca, into the shallow female genital atrium 50 μ posterior to that of the male (Figs. 37, 38).

The vitellaria surround the testes in an irregular annular ring. They extend anteriorly beyond the testes and are present behind the ovary as a group of post-ovarian vitellaria. In size these glands measure from 52 to 73μ in length and 24 to 38 μ in width. The two main vitelline ducts

lie in the lateral medullary parenchyma. They pass the ovary medianly and unite to form a single common vitelline duct, which connects with a single duct from the post-ovarian vitellaria, before disappearing into the oötype to unite with vaginal-oviducal canal to form the uterus. The uterus proper takes its origin just ventral to the spot where the vagina empties into the oviduct forming the vaginal-oviducal canal which is formed by the juncture of the common vitelline duct ventral to the vagina. After making several convolutions the uterus passes into a deep "U" shaped semicircle, surrounded by much loose glandular material. This structure is part of the oötype and shell gland. Several specimens show eggs in the process of shell formation. The whole series of ducts are at this point filled with vitelline material. The uterus remains thin walled as it leaves the shell gland and oötype and passes laterally and anteriorly. As the posterior tip of the right half of the ovary is passed the uterus becomes surrounded by numerous deep staining pear shaped glandular cells. The exact function of these cells is not known. The uterus then proceeds medianly, still remaining on the right side and runs with several smaller convolutions dorsal to the oviduct. It makes several deep twists and then passes to the left side and its coils extend anterior to the cirrus sac where it undergoes numerous convolutions; eventually reaching a position posterior and dorsal to the cirrus sac. The uterus then descends rapidly, joins the vagina and passes as already described, into the female genital atrium. The eggs are small thin shelled and ovoid, non-operculate measuring 26 to 32 μ in length by 18 to 21 μ in width.

Hypocaryophyllaeus paratarius undeniably belongs to the Caryophyllaeinae and this therefore raises the question of a genus to hold this species. It resembles Caryophyllaeus in nearly all respects except the uterine coils which lie anterior to the cirrus sac, the presence of an external seminal vesicle, the longitudinal extent of the uterus in relation to that of the testes and the fact that it is found only in the Catostomidae. Likewise this form cannot be classed as a member of the genus Glaridacris on account of the uterine coils and the longitudinal extent of the uterus which is one-fourth or less that of the testes. *Hypocaryophyllaeus paratarius* in no wise resembles a species of the genus Monobothrium and it corresponds to Caryophyllaeides only in respect to the position of the uterine coils. It differs in type of ovary, length of the uterine coils in relation to the longitudinal extent of the testes, type of scolex and the host. The genus Biacetabulum, upon the other hand, differs from *H. paratarius* in possessing a Caryophyllaeides-like genital atrium and in being characterized by a distinct scolex bearing acetabular-like suckers. Since *H. paratarius* fits into none of the aforementioned genera the author erected a new genus, Hypocaryophyllaeus, to hold this form. (See Hunter 1927.)

GENUS ARCHIGETES LEUCKART 1878

Generic diagnosis: Caryophyllaeinae with well defined, hexagonal-shaped scolex, bearing two bothria-like depressions. Cirrus opens into the utero-vaginal canal before it reaches the surficial atrium (like Caryophyllaeides?). Ovary "H" shaped and medullary. Excretory system without terminal vesicle, but with numerous ampullae at the posterior end of body. Uterine coils extend anteriorly beyond the cirrus sac, and vas deferens expands to form an external seminal vesicle. Caudal vesicle carrying embryonic hooks. Parasitic in body cavity of Tubificidae.

Type species: *Archigeters sieboldi* Leuckart 1878.

To include: (1) *A. sieboldi* Leuckart 1878. (2) *A. brachyurus* Mrázek 1908. (3) *A. cryptobothrius* Wisniewski 1928.

SUBFAMILY LYTOCESTINAE HUNTER 92 7

Subfamily diagnosis: Caryophyllaeidae with sexual apertures and ovary situated in the last quarter of the body length. The inner longitudinal muscles lie *entirely internal* to the vitellaria which are annularly arranged about the muscles in the cortical parenchyma. Uterine glands are present.

Type genus: Lytocestus Cohn (1908).

GENUS LYTOCESTUS COHN 1908

Generic diagnosis: Lytocestinae in which the scolex is unspecialized and not broader than the remainder of body. Male and female genital pores open on the surface behind one another and not into a common atrium. Two rows of main longitudinal muscles, the outer one being cortical and internal not external to the nuclear layer of subcuticula. Longitudinal extent of the uterus is at the most one third that of testicular field. Ovarian follicles cortical, only ovarian commissure being medullary. Uterus does not extend anterior to wings of ovary which is "H" shaped. Post-ovarian vitellaria absent. Parasitic in Mormyridae and Siluridae.

Type species: *Lytocestus adhaerens* Cohn, 1908.

To include: (1) *L. adhaerens* Cohn, 1908. (2) *L. filiformis* (Woodland, 1923). (3) *L. indicus* (Moghe, 1925).

At the present time this genus constitutes a refuse pile into which are cast many questionable forms. Some belong here without question. Such for example is the case of *L. filiformis* (Woodland 1923). Fuhrmann and Baer (1925) placed this form in the genus Lytocestus, along with *L. chalmersius* (Woodland 1924). These authors state at the time that while the descriptions of both forms are inadequate they clearly belong to

the genus Lytocestus. However, from reading a description of *L. chalmersius* this author feels very strongly that a restudy of the parasite in question may lead to its being placed in the new genus created by Fuhrmann and Baer (1925), Monobothroides. In the first place, the type of scolex is the same in both forms, as each possesses a terminal introvert and a number of furrows extending longitudinally. Further than this the arrangement of the reproductive organs appears essentially similar, so that this author feels confident that it really belongs in the genus Monobothroides. The writer has therefore tentatively placed this form in the aforementioned genus.

Woodland (1926) suggests that Moghe's "*Caryophyllaeus*" *indicus* probably belongs in the genus Lytocestus. Allowing for the misinterpretation of several structures it appears quite probable that the form really does belong in that genus, altho it should be redescribed in greater detail. On the authority of Woodland (1926) the writer placed Johnston's (1924) "*Balanotaenia*" *bancrofti* in the same group (Hunter 1927). Since then access to the original paper of Johnston has established the validity of the genus (Hunter 1929). According to Woodland (1926) the "*Caryophyllaeus*" *noliticus* of Kulmatycki (1924) is *W. virilis* Woodland 1923.

GENUS BALANOTAENIA JOHNSTON 1924 char. emend.

Generic diagnosis: Lytocestinae (?) possessing little specialization of the scolex, except longitudinal loculi and a circular muscular "frill" which is folded and thick when contracted. Male reproductive system opens separately or into a common genital atrium on the ventral surface. Ovary "H" shaped and only the isthmus (ovarian commissure) is entirely medullary. Main inner longitudinal muscles lie partially *internal* to the testes as two parallel sheets frequently broken up by strands which go about and between the testes. Uterine coils do not extend anteriorly to the cirrus sac and have a maximum length less than one-half the length of the testicular field. Post-ovarian vitellaria absent. Parasitic in the intestine of Siluroids. Development unknown.

Type and at present only species: *Balanotaenia bancrofti* Johnston 1924.

As noted above *Balanotaenia bancrofti* was relegated to the genus Lytocestus in a previous publication (1927) on the authority of Woodland (1926). At that time this author did not know the location or publication of the original description of this parasite. Since locating the work it appears that the genus belongs in the "Lytocestus group" and hence falls into the subfamily Lytocestinae. Likewise it is apparent that there are sufficient characters to warrant the retention of this form as a valid genus.

GENUS MONOBOTHROIDES FUHRMANN AND BAER 1925

Generic diagnosis: Lytocestinae with scolex devoid of bothria, but bearing numerous longitudinal furrows, and possessing a terminal introvert. Male and female reproductive systems open on the surface by two separate pores. Uterus never passes anteriorly to the cirrus sac and is present as a long regularly wound tube. Post-ovarian vitellaria absent. Ovary "H" shaped, coils of uterus extend anterior to wings of ovary. External seminal vesicle present. Parasitic in the intestines of the Siluridae.

Type Species: *Monobothroides cunningtoni* Fuhrmann and Baer, 1925.
To include: (1) *Monobothroides cunningtoni* Fuhrmann and Baer, 1925.
(2) *Monobothroides chalmersius* (Woodland 1924) (?).

As noted previously *L. chalmersius* is provisionally placed in this genus by this author on the basis of the scolex with a terminal introvert and the numerous longitudinal furrows. The male and female reproductive systems open separately. Unfortunately the exact position of the uterine coils in relation to the cirrus sac could not be ascertained from Woodland's figures, but the uterus appears to be regularly coiled. There are no post-ovarian vitellaria, the ovary is "H" shaped and the uterine coils extend anteriorly to the wings of the ovary. The presence or absence of an external seminal vesicle could not be determined. There appear to be enough characters to warrant placing this species provisionally in the genus, for it is certainly more closely allied to it, than to Lytocestus.

GENUS DJOMBANGIA BOVIEN 1926 Char. emend.

Generic diagnosis: Lytocestinae with globular scolex armed with terminal sucker, circular in shape bearing acetabular affinities. Male and female reproductive systems open into common genital atrium near the posterior end of body (?). Ovary "H" shaped, entirely medullary (?). Uterine coils extend anteriorly to cirrus sac nearly as far as testicular field thus forcing testes to edges of medullary parenchyma. Post-ovarian vitellaria absent. Eggs covered with spines. Parasitic in intestine of Clarias sp. Development unknown.

Type and at present only species: *Djombangia penetrans* Bovien 1926.

This genus clearly belongs in the subfamily Lytocestinae altho several of its diagnostic characters could not be definitely determined from the original description of Bovien (1926). Thus the figures show beyond doubt the location of the sexual apertures as well as the position of the vitellaria in relation to the inner longitudinal muscles. Furthermore the uterine glands are present in this form. In the generic diagnosis it was impossible to determine whether or not the ovary was entirely medullary for no sections were given which showed this. Judging from the location of the

vitellaria and the testes in the toto mount it was possible to deduce that the ovary would be medullary rather than cortical in position. Another point which could not be ascertained from the figures of Bovien (1926) is whether or not the male reproductive system opens into the female utero-vaginal canal or into a common atrium. The figure leads one to the conclusion that the male system opens into the female, for it more closely resembles the type of atrium described for Caryophyllaeides Nybelin (1922) than Caryophyllaeus.

GENUS LYTOCESTOIDES BAYLIS 1928

Generic diagnosis: Lytocestinae with short conical scolex, not broader than the rest of the body and devoid of bothria. Vitellaria superficial, forming a continuous layer which surrounds the testes and other organs and continue laterally to post-ovarian vitellaria. Testes arranged internally to the vitellaria, usually forming a layer. Male and female reproductive systems open into shallow common genital atrium in the last fourth of the body length. Uterus relatively short. Excretory canals, at least in the posterior region of the body, internal to the vitellaria. Parasitic in the digestive tract of a fish (probably Alestes sp.). Development unknown.

Type and at present only species: *Lytocestoides tanganyikae* Baylis 1928.

In the original description of this genus and species Baylis noted that the material was in a poor state of preservation. Hence many of the details of the musculature, etc. could not be made out. Baylis (1928) noted the proximity of the vitellaria to the body surface as well as the location of the excretory canals internal to the vitellaria. These he pointed out were reasons for supposing that the inner longitudinal muscles were probably located internally to the vitellaria, since in all other species the main longitudinal muscle system lies about, or in the medullary parenchyma and the excretory canals are external to this. Another indication that this genus belongs in the Lytocestinae lies in the regular shape of the vitellaria. This author pointed out (Hunter 1929) that the vitellaria were only irregular in shape when they were squeezed in passing between the strands of the inner longitudinal muscles to reach the cortical parenchyma. Since this condition is only found in the Capingentinae (Pseudolytocestinae) where these glands have a medullary origin their regular shape in the case of this genus may be taken as additional evidence of their belonging in the Lytocestinae.

SUBFAMILY CAPINGETINNAE NEW SUBFAMILY

SYNONYM: *Pseudolytocestinae* Hunter 1929

Subfamily diagnosis: Caryophyllaeidae with sexual apertures and ovary situated in last fifth of the body. The inner longitudinal muscles *partly*

internal to vitellaria which arise and extend for one third to one half their length in medullary parenchyma where they are typically annularly arranged about the muscles in cortical parenchyma. Uterine glands present.

Type genus: Capingens Hunter 1927.

The only difference between this subfamily and the Lytocestinae lies in the relation of the vitellaria to the inner longitudinal muscles. In cases where the separation is clear cut we find the muscles functioning as a complete wall or sheath. In the case of this subfamily the vitellaria originate within the inner longitudinal muscles but much of their bulk is forced between the strands of the muscles and so extrude into the cortical parenchyma for one third to one half their bulk. Since this difference is constant in the various genera and species and differs from the Lytocestinae proper it appeared advisable to create a new subfamily and place therein all the genera possessing vitellaria which extrude into the cortical parenchyma for one third to one half their bulk. This was done in a previous paper (Hunter 1929). Phylogenetically this subfamily no doubt lies between the Caryophyllaeinae and the Lytocestinae. Since Capingens was the first genus of this group to be described it was taken as the type genus (Hunter 1929). At that time the group was erroneously designated as Pseudolytocestinae which was of course incompatible with the assignment of Capingens as the type genus.

GENUS CAPINGENS HUNTER 1927

Generic diagnosis: Capingentinae possessing a definite scolex which occupies one-fifth to one-fourth total body length and bearing one pair of well defined bothria. The scolex does not vary in shape as in the other Cestodaria. Vitellaria extend into cortical parenchyma past inner longitudinal muscles having their origin within medullary parenchyma. These glands form a continuous row laterally with post-ovarian vitellaria. Cirrus opens on ventral surface or into a shallow genital atrium which is non-eversible and is anterior to similar atrium for female system. Uterine coils lie anteriorly to cirrus sac and reach a maximum longitudinal extent of one-third or less that of testicular field. External seminal vesicle present. Parasitic in *stomach* of Catostomidae. Development unknown.

Type and at present only species: *Capingens singularis* Hunter 1927.

Capingens is one of the most interesting genera of the Caryophyllaeidae. Upon first examining the scolex one is impressed with the superficial similarity to the Bothriocephalid tapeworms. Further study serves only to accentuate the likeness which is primarily one of musculature. Sections of the scolex of *Capingens singularis* compares very closely with that of *Bothriocephalus microcephalus Rud.* Indeed within this group lies

real morphological evidence of a relationship between the Caryophyllaeidae, the Ptychobothriidae and the Cyathocephalidae. Here the likeness ends for the remainder of the organization of the parasite is clearly that of the Caryophyllaeidae.

As noted in a previous publication (Hunter 1929) this genus was removed from the Lytocestinae where it was originally placed and taken as the type genus of the Capingentinae. At the time of the original description note was made of the medullary origin of the vitellaria, but it was not until several more forms were discovered with a similar arrangement that any systematic significance was placed upon it. After further study these were all grouped together in the subfamily, Capingentinae. The genus name was formed from "caput" and "ingens" to denote the great size of the scolex.

CAPINGENS SINGULARIS HUNTER 1927

[Figs. 10, 11, 35, 73–77]

1927: *Capingens singularis*	Hunter 1927: 24
1928: *Capingens singularis*	Baylis 1928: 561
1929: *Capingens singularis*	Hunter 1929: 186

Specific diagnosis: With the characters of the genus. Adult parasites ranging from 4 to 8 mm. in length and 1.08 to 1.5 mm. in maximum breadth (which occurs in the scolex). Neck indistinct and is in reality absent for the reproductive organs extend into the base of the scolex. Maximum body width (exclusive of the scolex) is 1.23 mm. Body oval in cross section; cuticula 3 to 4 μ in thickness. Subcuticula 5 to 6 μ deep, followed by the cortical parenchyma which is 30 to 45 μ across. Inner and outer longitudinal muscles present although the latter are not prominent. Testes are 210 and 225 in number and have a maximum diameter of 0.06 to 0.108 mm. Cirrus sac round, occupies three-fourths of the medullary parenchyma and is from 0.216 to 0.264 mm. in diameter. Circular muscles 24 to 36 μ in thickness. Male and female reproductive systems open on the surface 60 to 70 μ apart. Vagina convoluted, does not form a receptaculum seminis. Ovary globular and very short, nearly surrounding the cirrus sac, 0.25 to 0.35 mm. in length; possesses an extremely narrow ovarian commissure only 24 to 36 μ in diameter. Oviduct 80 to 90 μ. Vitellaria take their origin in the medullary parenchyma but extend past the inner longitudinal muscles and into the cortical parenchyma, and are 36 to 60 μ by 14 to 24 μ. Excretory canals numerous and average about 25 to 30 pairs of longitudinal canals in cross section. Excretory vesicle 40 μ by 19 to 24 μ and lies in a horizontal plane. Ovoid eggs 40 to 45 by 21 to 26 μ.

Host: stomach of *Carpiodes carpio*, Rock River, Illinois, and *Ictiobus urus*, Lake Pepin, Minnesota.

Type: Slide No. 29.46 in the collection of Dr. Henry B. Ward.

Paratype: Slide No. 422.1 in the collection of the author.

Host	Locality	Collector	Authority
Carpiodes carpio (Rafinesque)	Rock River, Rock Falls, Ill.	G. W. Hunter, III and H. E. Essex	Hunter (the present paper)
Ictiobus urus (Agassiz)	Mississippi River, Lake Pepin, Minn.	G. W. Hunter, III and H. E. Essex	Hunter (the present paper)

Two specimens of *C. singularis* were obtained in examinations covering nearly six hundred fish of the family Catostomidae. It is evident that this species is rare and occurs infrequently in the genera of fish examined. However, the habitat and external appearance of this parasite mark it as unique among the Caryophyllaeidae. It is found embedded between the folds of the mucosa and submucosa in the stomach of its host. During the summer of 1925 *C. singularis* was first encountered in the stomach of *Carpiodes carpio* taken from the Rock River at Rock Falls, Illinois. (Essex and Hunter (1926) give a general account of this expedition.) Later, while at Lake Pepin on the Mississippi River another specimen was found in the stomach of *Ictiobus urus*. Both hosts were of good size, the first measuring 25 cm. and the other 50 cm. One specimen was stained and mounted in toto, the other was sectioned.

Capingens singularis is very regular in shape. The scolex is large, prominent and measures about 1.13 mm. occupying one-fourth of the body length. On the dorsal and vental surfaces of the scolex are immense bothroid suckers measuring 0.8 to 1.03 mm. in length (Fig. 10). Behind these suckers is a constriction indicative of the neck. The body gradually becomes more pointed as the posterior tip is approached, which is bluntly rounded. The length of this species varies from 4.22 to 6 or 8 mm.; the maximum width which occurs in the scolex is 1.08 to 1.53 mm. The neck measures 0.7 to 0.9 mm. while the maximum body width is 1.23 mm. The width anterior to the cirrus sac is about 0.6 mm. while posterior to it the breadth is 0.55 mm. Several other distinguishing characters can be seen in a toto mount. The vitellaria are small and lie in 10 to 15 rows paralleling the longitudinal axis. The testes are unusually small lying in 7 to 8 parallel rows. The cirrus sac is prominent and the coils of the uterus extend anteriorly to it.

The scolex of this species is very prominent and occupies about one-fourth of the body length (Fig. 10). It is roughly rectangular in shape, bearing two large and deep efficacious suckers upon its flattened dorsoventral surface. These suckers are distinctly bothroid and are of immense

size. As has been noted in the preceding paragraphs it extends in a posterior direction and measures from 0.8 to 1.0 mm. in length and 0.5 to 0.6 mm. in width. The depth of this sucker is from 0.15 to 0.25 mm. The following table gives a summary of the measurements based on the toto mounts and the cross sections of the specimens. The musculature of

Measurements of Suckers of C. SINGULARIS

Length (anterior-posterior)	0.8 –1.0 mm.
Breadth (at surface)	0.5 –0.6
Breadth (at base of sucker)	0.20–0.30
Depth of sucker	0.15–0.25

the scolex and the sucker is of interest. The inner longitudinal muscles are very prominent and numerous fasciculi are present, each containing as many as fifty individual muscle fibers. These bundles of muscles penetrate into the scolex, which is much wider than the body. The inner longitudinal muscles start curving towards the cuticula. Many of these become lost in the basement membrane of the posterior portion of the sucker (Fig. 11). Other fibers continue anteriorly. The cuticular muscles of the scolex surrounding the suckers become highly specialized for the circular layer has thickness of 20 to 30 μ. Likewise the longitudinal cuticular muscles are highly developed and may be seen throughout the scolex as dorso-ventral and lateral muscle fibers. The former connect the suckers back to back, while the latter run from their sides to the lateral portions of the scolex (Fig. 11). The scolex resembles a capital "I" in cross sections. The remaining fibers of the inner longitudinal system are found medianly as the suckers deepen, and those which are not inserted from time to time on the basement membrane of the suckers ultimately reach the more distal portions of the scolex. A few of the longitudinal muscle fibers become specialized as diagonal muscles. The cells of the parenchyma are scattered throughout the scolex indiscriminately. The canals of the excretory system are present in the base of the scolex and extend anteriorly for some distance as canaliculi but do not break up into as many canaliculi as in *M. ingens*. The descending branches unite to form the main descending excretory canals. No neck is present, for in both specimens the reproductive organs first appear in the base of the scolex.

The cuticula is composed of a layer 3 to 4μ in thickness of which the lower third goes to form the basement membrane. The cuticula becomes slightly thinner in the scolex, although at this point the muscles of the scolex become highly specialized. In the median and posterior body parts the circular cuticular muscles form a layer less than 1 μ in width, beneath which are found the longitudinal muscles of the same system. Between the basement membrane and the outer longitudinal muscles lies the subcuticula. This layer is non-nucleate and is largely filled with connective tissue and lateral or dorso-ventral muscle fibers which branch

before passing between the longitudinal cuticular muscles to their insertions on the basement membrane. This subcuticular layer is only 5 to 6 μ in thickness and its limits extend from the basement membrane to the beginning of the nucleated cortical layer and the few scattered outer longitudinal muscles of the parenchyma. These occur in small groups some 30 to 45 μ outside the inner longitudinal system. This latter very prominent group marks the beginning of the medullary parenchyma. Within the cortical layer are found the main tubes and tubules of the excretory system. The greater number of the vitellaria lie externally to the inner longitudinal muscles, and external to these are the canals of the excretory system surrounded with masses of nuclei. There are also numerous round parenchymal cells; these have a heavy cell wall and the nuclei stain deeply. Numerous myoblastic cells are also present.

The arrangement of the musculature of *C. singularis* is somewhat unusual. The cuticular muscles are quite indistinct except in the scolex. They are composed of the circular and longitudinal sets of fibers; the former lying close beneath the basement membrane and the latter situated medianly to the circular layer. In the scolex both sets of fibers become highly developed, especially in the region of the acetabular suckers, where the circular muscles develop into a layer 20 to 30 μ in thickness. Likewise the bulk of the fibers which connect the backs of the suckers and those extending to the more lateral portion of the scolex arise from the longitudinal cuticular system. Five to 6 μ from the basement membrane are found the outer layer of the longitudinal parenchymal muscles. Several fibers are grouped together and lie just externally to the nucleate cortical parenchyma. These fibers are more plentiful in the anterior parts of the body and are found in greater numbers near the dorsal and ventral surfaces. Where these muscles are found in the posterior body parts they often appear as single strands; this is particularly true of the region about the cirrus sac and posterior to it. The inner longitudinal muscles are readily distinguished for they stand out with great clarity. Lying 30 to 45 μ more medianly than the outer longitudinal muscles and having as many as 50 or more individual fibers in each fasciculus they dominate the field so as to readily attract the eye. These large groups of muscles measure between 16 to 32 μ in greatest diameter (Fig. 73). The disposition anteriorly of these muscles has been described in detail in the paragraphs dealing with the scolex and will not be reconsidered here. Posteriorly the inner longitudinal fibers gradually converge so that as the excretory vesicle is reached they assume a position about this cavity, the majority of these muscles becoming embedded in its walls. However a few extend past this cavity and are attached to the basement membrane in the posterior extremity. Dorso-ventral and lateral muscles fibers are present in considerable numbers throughout the body. Both sets of fibers inter-

mingle freely with those of the inner longitudinal system. The dorso-ventral fibers are present in greater numbers than those of the lateral system; they aid in keeping the body shape of the parasite and also in holding the reproductive organs in position.

The excretory system is comprised of a series of main ascending and descending canals, the former are situated closer to the surface than the latter. In general the entire system resembles that described by Fraipont (1880) for Caryophyllaeus. The ascending canals are smaller than those of the descending system and are formed by small canaliculi which in turn are composed of several renal corpuscles uniting to form the caniculus. These cells are not the typical flame cells but resemble the renal corpuscle described by Cooper (1920). These are large cells, and take a deeper stain than the parenchyma. They are round with radiating fibers of cytoplasm extending out to the wall of the vesicle in which they lie. These fibers take a lighter stain than the remainder of the cell body and some take an eosin counter stain. This suggests the possibility that these renal corpuscles, which lie at the expanded distal end of a canaliculus, contain muscular fibrillae which have the ability to contract and in so doing force the liquid wastes accumulated in this cavity out through the canaliculus to the ascending canal. Evidence for this view may be found in the way these cells or portions of them took the counter stain, and also by the fact that a few of these cells are found in a more contracted state than some of the others which was indicated by a thickening of the fibrillae and the walls of the ducts lying closer to the walls of the renal cell. As is the case with the flame cell the renal corpuscle caps the expanded portion of the canaliculus, only a portion of it lying in the cavity of the canal itself (Fig. 77).

Both series of canals are so irregular in their course that it was impossible to determine the number of main ascending or descending canals. In one cross section, for example, the number of times the descending canals are cut numbers over thirty. This is typical of the sections. In the scolex the ascending canals are scarcely broken up and do not permeate the scolex as is the case in some of the other species described. This fact may be interpreted as evidence for the view that the excretory system plays a part in the extrusion of the scolex, which in this species shows but little movement when living material is studied.

The descending canals extend posteriorly and lie within 10 to 20 μ of the inner longitudinal muscles passing into the excretory vesicle from the side. This vesicle lies horizontally, 70 μ from the outside, measures 40 μ in length and has a maximum diameter of 19 to 24 μ. The bulk of the inner longitudinal muscles become attached to the sides of the excretory vesicle. Apparently it is derived from the outer layers for the cuticula is continued as a lining of the vesicle. It narrows posteriorly and passes at right angles into a narrow canal leading to the ventral surface. This canal

is 42 to 50 μ long and 4 to 9 μ wide; it is slightly inclined towards the posterior tip. This canal in turn empties into a large excretory atrium which is 36 to 48 μ in diameter and 20 to 30 μ in depth. The atrium and the canal emptying into it are lined with cuticula identical with that found elsewhere on the surface of the parasite.

The testes are small, irregularly lobed and lie within the inner longitudinal muscles. They are arranged in an irregular single row, sometimes so irregular that it appears as two. The long axis of the testes is in a dorsoventral plane. These glands alone are found within the inner longitudinal muscle layer, for the vitellaria, while having their origin median to the muscles, soon grow between these fasciculi and so extend into the cortical parenchyma (Fig. 73). The testes range in size from 0.060 to 0.108 mm. in length to 0.048 to 0.072 mm. in width. The number in trans-section varies from 8 to 16. The mitotic figures show with almost diagrammatic clearness. The number of testes range from 210 to 225 and was determined by an estimation of their number. The vas deferens is first clearly distinguishable in the region just posterior to the center of the body length. The vas deferens is formed medianly about 1.3 mm. anterior to the cirrus sac. It is formed by the union of three smaller ducts, evidently canals of the *vasa deferentia secondaria*. It is soon crowded ventrally by the coils of the uterus lying anteriorly to the cirrus sac. In toto mounts of the ventral surface the entire region filled with the vas deferens is blocked off as an inverted capital "U." This duct passes posteriorly through numerous convolutions. The diameter of the tube is small and the width varies from 16 to 24 μ. The testes disappear from the center of the field with the advent of the vas deferens and the uterine coils. However, they still persist laterally, leaving the median 0.2 mm. of the medullary parenchyma to the developing tubes of the reproductive systems. As the cirrus sac is approached the inner longitudinal muscles are pushed nearer the surface thus bowing out the muscles of that region. Shortly before this organ is reached the vas deferens winds medianly and passes into a small narrow ductus ejaculatorius. This canal is surrounded by circular muscles which in turn are surrounded by cells which do not stain as deeply as those about the uterus and so may readily be distinguished from them. The ductus ejaculatorius passes ventrally where it forms a seminal vesicle. This structure is 84 μ in length and 60 μ in width. The cavity itself lies in a nearly horizontal plane and is 52 by 14 μ. Upon leaving the seminal vesicle the ductus ejaculatorius doubles back upon itself towards the middle of the body where it penetrates the median anterior wall of the cirrus sac. Around this entire region are numerous muscle fibers which leave the inner longitudinal muscle band to form an almost unbroken layer of muscles surrounding the muscular cirrus sac and the uterine coils above. The cirrus sac is round and having a diameter of

0.21 to 0.26 mm. The circular muscles are 24 to 36 μ in thickness and evenly distributed (Fig. 74). Retractile fibers for the withdrawal of the cirrus are also present, although not in great numbers. The limits of the cirrus sac do not extend beyond the inner longitudinal muscles. At this point 30 μ from the outside, the cirrus sac empties into the middle of the male genital atrium. This atrium is 40 μ in length and 30 μ in breadth at the surface. It extends dorsally for 60 μ surrounding the ventral portion of the cirrus sac; in other words the lower portion of the cirrus sac protrudes into the male genital atrium. The extruding cirrus of the parasite in toto mount gave the following measurements:

length	0.30 mm.
width at apex	0.072 mm.
width in middle	0.108 mm.
width at base	0.144 mm.

The apparent discrepencies in measurements between the width of the cirrus and the diameter of the male genital atrium indicates that it is capable of considerable expansion. The female reproductive system opens to the surface in a female genital atrium. The anterior border of this cavity is 30 μ posterior to the closest edge of the male atrium and the centers of these two cavities lie approximately 60 to 70 μ behind each other (Fig. 75).

The female reproductive system of *C. singularis* is unusual in several details and therefore is of particular interest. In the first place, the uterus extends anteriorly to the cirrus sac and in the second, the coils do not reach posteriorly beyond the level of the oötype. The position of the vitellaria is also unique. All of these facts coupled with others of lesser importance mark it as one of the most interesting species encountered. The ovary is lobular and is confined to the lateral third of the medullary parenchyma. It is not as long as those of other species, measuring from 0.25 to 0.35 mm.; the maximum width is about 0.19 mm. The ovary extends to the anterior side of the cirrus sac; it assumes an "H" shape with the ovarian commissure exactly in the middle. But this commissure is much weaker than is normally the case for its diameter varies from 24 to 36 μ.

The oöcapt arises from the posterior ventral margin of the ovarian commissure, slightly to the right of the center. It is 14 μ wide with circular muscles 2 to 3 μ thick surrounding this canal for 10 to 12 μ. The oviduct arising from the distal extremity of the oöcapt is relatively long and measures, not including the oöcapt, 80 to 90 μ. It passes ventrally and winds to the left just within the boundary of the oötype whose cells permeate this entire region from the ovarian commissure to the post-ovarian vitellaria. The maximum width reached by the oötype is 0.216 mm. This may vary in different specimens but it fills the entire medullary parenchyma dorso-

ventrally, and within its confines are found the vagina, vitelline ducts, oviduct, and the beginnings of the uterus (Fig. 35).

The center of the female genital atrium lies 60 to 70 μ posterior to that of the male. This atrium only lies 80 μ anterior to the ovarian commissure. It extends dorsally for 0.115 mm. and at this point it divides into two ducts, one the vagina, passing to the right, and the other the uterus, entering from the left. These ducts empty near the middle of the body (Fig. 75). The vagina is median and soon coils dorsally above the center of the body passing anteriorly and then posteriorly. It shortly forms an arc across the dorsal portion of the anterior edge of the oötype and passes ventrally and to the left where it is joined by the oviduct from below. The vagina does not expand to form a receptaculum seminis. The duct is lined by a thin cuticula-like membrane about which is a layer of circular muscles. These in turn are surrounded by cells, the myoblasts of the muscle layer. The vitellaria are of particular interest for several reasons. In the first place they are very small, measuring from 36 to 60 μ by 14 to 24 μ. These glands originate from the medullary parenchyma, but they grow towards the surface. Their general shape, therefore, resembles an Indian club, or a Florence flask, with the smaller neck situated medianly and the bulk of the gland lying outside of, or between, the inner longitudinal muscles. As the vitellaria are small they are present in greater numbers (Fig. 73). This is evident from the toto mounts where as many as 13 to 15 rows may be counted on one surface (Fig. 35). These rows are continuous longitudinally and present an unusual appearance which is characteristic for the species; they connect at the lateral margins with the post-ovarian vitellaria. The vitelline ducts are numerous and lie within the medullary parenchyma. The main ducts are situated laterally for all of the others converge to these two which in turn are joined by those from the post-ovarian vitellaria. These combined vitelline ducts parallel the ovary where they unite medianly to form a single duct. It is this vitellarian canal which penetrates the oötype, passes ventrally, and finally dorsally to unite with the combined vaginal-oviducal canal, or fertilization chamber. In this species this chamber is 50 μ in length. With the juncture of the common vitelline duct the uterus is formed which soon passes obliquely dorsal and is surrounded with glandular cells as well as circular muscle fibers. The lining of this portion of the canal is unusual for it appears striated with these striations caused by protrusions into the duct. The wall is composed of cells between which empty ducts from the glandular cells. Circular muscle fibers lie scattered between the cells lining the canal while radiating longitudinal muscle fibers are also present. It is probable that the cells lining the canal are glandular and it is evident that those lying at some distance from the canal are also glandular in nature (Fig. 76). The uterus makes several convolutions through

the oötype, turns anteriorly and soon leaves the confines of the oötype. Even before leaving this organ the deep staining glandular cells which typically surround the uterus appear. This canal passes anteriorly keeping a position dorsal to the cirrus sac until beyond it where it becomes more convoluted. The uterus passes 0.36 mm. anterior to the cirrus sac and dorsal to the vas deferens. It has two main branches, the ascending and descending uterine limbs. These may sometimes become so convoluted that three or four portions of the uterus appear in cross section, though always in the dorsal half of the body. The glandular walls of the uterus are found throughout its entire length, the cells even persisting until the duct empties into the female genital atrium. The eggs of this species are small and ovoid. Only a few were present and these varied in size from 40 to 45 μ in length by 21 to 26 μ in width.

Capingens singularis clearly belongs in the family Caryophyllaeidae and the position of its sexual aperature, ovary and the presence of the uterine glands place this form in either the Capingentinae or Lytocestinae. In view of the extension of the vitellaria past the inner longitudinal muscles and into the cortical parenchyma *C. singularis* clearly goes into the former. There are two other genera in this subfamily, Pseudolytocestus Hunter 1929, and Spartoides Hunter 1929. The main point of difference between the two is in the type of scolex which in the case of the latter resembles the scolex of Hypocaryophyllaeus. The massive scolex of *C. singularis* occupies one-fourth the body length and possesses a deep bothria-like sucker on the dorsal and ventral surfaces. This together with the Caryophyllaeides-like uterus and the presence of post-ovarian vitellaria clearly separate it from either Pseudolytocestus or Spartoides. Yet it belongs in this subfamily as was shown above, and the author therefore created a new genus, Capingens, to hold this form (Hunter 1927). Originally this genus was placed in Lytocestinae, but was transferred to the Capingentinae on the basis of the vitellaria in relation to the inner longitudinal muscles when this new subfamily was created. It is taken as the type genus of the subfamily.

GENUS PSEUDOLYTOCESTUS HUNTER 1929

Generic diagnosis: Capingentinae possessing little specialization of scolex. Cirrus opens separately on ventral surface or into a shallow eversible genital atrium. Ovary "H" shaped, almost entirely medullary, only one third of the ovarian follicles extend into cortical parenchyma. Uterine coils never extend anteriorly to cirrus sac, with a maximum length of one third that of testicular field. Post-ovarian vitellaria absent. Parasitic in the intestines of the Catostomidae. Development unknown.

Type and only species: *Pseudolytocestus differtus*, Hunter 1929.

This genus differs from Monobothrium primarily in that the vitellaria are not entirely medullary, the cirrus sac does not open via a distinct genital papilla and there are no loculi nor distinct terminal introvert on the scolex. Neither can it be made a synonym for either Spartoides or Capingens, as the ovary alone in the former and the scolex of the latter would be sufficient to exclude this form from both. Since this form fitted none of the available genera of the Pseudolytocestinae it was necessary to create a new genus to hold it. Because of the superficial resemblance of this to the genus Lytocestus the new genus is named Pseudolytocestus.

PSEUDOLYTOCESTUS DIFFERTUS HUNTER 1929

[Figs. 23, 26, 52, 71, 91]

1929: *Pseudolytocestus differtus* Hunter 1929: 188.

Specific diagnosis: With characters of genus. Adult parasites free in intestine, length 10 to 20 mm.; width 0.6 to 1.7 mm. Neck distinct and short, 0.9 to 1.7 mm. long by 0.6 to 0.95 mm. wide. Musculature of scolex generally resembles that of *C. terebrans*. No external longitudinal grooves present. Body broadens posteriorly and is oval in cross section. The cuticula tripartite, outer stainless and tubercular, inner takes eosin, lined with basement membrane; composite 8 to 10 μ thick. Subcuticula 15 to 20 μ deep, bounded medianly by the cortical layer of the parenchyma which is 68 to 81 μ in depth. Cuticular and parenchymal muscle systems present and prominent. Testes number 725 to 775, are roughly oval and have a maximum diameter of 0.13 to 0.2 mm. Cirrus sac and external seminal vesicle form the Greek letter "Λ," joining dorsally. Cirrus sac forms an angle of less than 30 degrees with the vertical, fills entire medullary parenchyma dorso-ventrally, being 0.2 to 0.5 mm. long. The circular muscles of this organ are weak. Female genital atrium opens on ventral surface 0.27 to 0.3 mm. posterior to the male orifice. Utero-vaginal canal 0.16 to 0.34 mm. long, extending dorsally; uterus empties at middle of body from the right. Vagina proper extends dorsally 0. 4 to 0.6 mm. until close to the dorsal layer of the medullary parenchymal muscles. It passes ventrally and does not form a receptaculum seminis. Wings of the ovary are 0.6 to 1.35 mm. long and 0.2 to 0.4 mm. wide; these extend out past the inner longitudinal muscles in same manner as the vitellaria; ovarian commissure entirely medullary, 0.23 to 0.27 mm. in diameter. Vitellaria measure 0.13 to 0.2 mm. in maximum diameter, are very irregular in shape extending past the inner longitudinal muscles into the cortical parenchyma (as in *C. singularis*). Eggs large, ovoid from 58 to 65 by 35 to 40 μ.

Host: *Ictiobus bubalus*, Tallahatchie River, Mississippi. In intestine.

Type: Slides No. 29.47 in the collection of Dr. Henry B. Ward.

Paratype: Vials and slides in the author's collection No. 651.3–651.5

Host	Locality	Collector	Authority
Ictiobus bubalus (Rafinesque)	Tallahatchie River, Money, Miss.	Parke H. Simer	Hunter (the present paper)

This material was found in only four specimens of *Ictiobus bubalus* examined by Dr. Parke H. Simer at Money, Mississippi and then only three or four individual parasites which were often mixed with other species in each host. One host, for example, contained several hundred *B. giganteum* and only two *P. differtus*.

This parasite possesses a scolex which is clearly demarked from the remainder of the body, being smaller and superficially resembling that of *C. terebrans*. The base is conical and regular and bears no definite indication of loculi or suckers (Fig. 23). Its length varies from 0.6 to 0.95 mm. while the breadth is 0.6 to 0.8 mm. The inner longitudinal muscles forming a terminal introvert are found attached in the region of the basement membrane of the distal extremity of the scolex. The muscles at the point of attachment to the scolex form an oval measuring 0.54 by 0.27 mm. As the inner longitudinal layer passes posteriorly through the scolex the muscles pass laterally so as to increase the area of the medullary parenchyma and in so doing decrease that of the cortical layer. The fasciculi of the inner longitudinal muscles continue as a ring from their insertion on the distal extremity of the scolex and pass posteriorly (Fig. 71). These fasciculi range from 15 to 40 μ in length and 13 to 15 μ in width. There are between 20 and 30 large individual fibers in each group. External to the inner longitudinal muscles lies the cortical layer of the parenchyma filled with nuclei and is 68 to 81 μ in depth and 25 to 30 μ from the exterior. This layer is bounded externally by the outer longitudinal muscles which are 4 to 6 μ thick and contain 3 to 6 individual muscle fibers per fasciculus. The subcuticula is relatively thin being only 15 to 20 μ and but 8 to 10 μ from the outside. In the outer limits of the subcuticula lie the relatively prominent longitudinal and circular muscles of the cuticular system. The outermost edge of the subcuticula is marked by the basement membrane of the cuticula about 1 μ thick and contains the circular cuticular muscles. External to this and taking an eosin stain is a smooth layer of material 4 to 5 μ thick while the outermost layer is but 3 to 4μ thick. This latter strip remains impervious to stain but is covered with a number of irregular granular tubercles scattered every

few micra throughout the layer. The neck does not possess any outstanding characteristics, being 0.9 to 1.7 mm. in length and 0.6 to 0.94 mm. in breadth. The excretory tubules are arranged in pairs as in other species. Contrary to many forms the maximum body width which varies from 0.9 to 1.2 mm. at the widest spot occurs just posterior to the neck and not in the region of the reproductive organs. The excretory system first appears in the anterior portion of the scolex where it is composed of the paired ascending and descending tubes. The former unite to form a ring from which the canals of the descending system take their origin. There are usually 10 pairs of main tubes altho some slight variation in this number has been noted. The descending canals terminate in a "T" shaped excretory vesicle located at the posterior tip of the body and varying in length from 0.1 to 0.16 mm. and in width from 0.025 to 0.03 mm. in the stem of the "T" and 0.1 to 0.13 mm. from tip to tip of the cross arms.

The small oval testes number between 725 and 775. This is by far the greatest number encountered and is explained by the relatively small size of these glands, 0.1 to 0.18 mm. long by 0.06 to 0.094 mm. wide (Fig. 91). The testes are arranged in two rows one dorsal to the other. The vitellaria surround them and are not found in the mid-region of the medullary parenchyma. The method used in the determination of the number present varies somewhat from the one typically followed. (Cf. page 11). Twenty testes picked at random were traced through to determine in how many sections they appeared. The average of these was taken and this number was divided into the total number of times that parts of testes were encountered in each section. This number, 4,537, divided by the average section number for each testis, 6, yields our number of 756, the number in this particular specimen. Several others were counted to check this and a second gave 750, and a third 759, so by allowing for variations and possible error we find the actual number is between 725 and 775.

Posteriorly the testes become pushed aside to make room for the coils of the vas deferens. This organ is surrounded throughout its course by a row of vitellaria and in addition it is usually flanked by four or five testes. The vas deferens may be said to occupy the middle third of the body. The maximum diameter of this organ varies from 0.067 to 0.168 mm. Ventrally the vas deferens gives way to the small muscular ductus ejaculatorius 0.04 to 0.06 mm. wide, the layer of surrounding muscles being 0.01 to 0.015 mm. thick. It arises 0.3 to 0.38 mm. anterior to the base of the seminal vesicle. Its path is tortuous, starting close to the ventral inner longitudinal muscles it winds dorsally for about 0.15 mm. and then ventrally for 0.1 mm. and finally dorsally and laterally passing into the lower end of the seminal vesicle. This organ is practically straight and lies in a dorso-ventral plane, forming the left arm of a Greek "Λ" at an angle

of about 30 degrees from the vertical. It is 0.35 to 0.45 mm. long and 0.15 to 0.2 mm. wide with prominent muscles 0.03 to 0.04 mm. thick. The cavity of the seminal vesicle is from 0.3 to 0.4 mm. by .075 to 0.093 mm. Along the base of the circular muscle layer are scattered cells which are 4.5 to 7.7 μ long. The seminal vesicle narrows and passes into a continuation of the ductus ejaculatorius which is less than 0.2 mm. long, which in turn passes into the long weakly muscled cirrus sac; this occupies all of the medullary parenchyma dorso-ventrally and one third laterally. It extends slightly posteriad forming the right arm of the Greek "Λ." The cirrus sac is ovoid being two to two and a half times as long as it is broad; it measures 0.2 to 0.8 mm. by 0.1 to 0.4 mm. (Fig. 26). Contrary to the usual situation the muscles of the cirrus sac are not concentrated along the outer edge and consequently do not form a definite band (Fig. 52). The distal extremity of the cirrus sac when extruded forms an irregular serrated margin thus resembling the genus Monobothrium (Fig. 52).

The female reproductive system usually opens on the surface or more rarely into a shallow atrium 33 to 67μ deep. The utero-vaginal canal extending dorsally for 0.13 to 0.27 mm. is close to the middle of the body. The uterus empties from the right at this point while the vagina continues dorsally until 0.4 to 0.6 mm. above the ventral surface. It then dips towards the ventral surface and passes posteriorly, keeping close to the ventral inner longitudinal muscles until the ovarian commissure is reached; the vagina passes up over this without forming a receptaculum seminis, dips ventrally and enters the oötype complex where it joins the oviduct to form the fertilization chamber.

The vitellaria are very irregular in shape for they extend past the inner longitudinal muscles much as they do in *C. singularis* (Fig. 91). Some few vitellaria may be found entirely external to this muscle layer while one or two are occasionally found entirely internal to it. The bulk of these glands, however, originate within the inner longitudinal muscles and push their way out past this layer to extrude for nearly one half their length into the cortical parenchyma (Fig. 91). The size varies from 0.08 to 0.17 mm. and 0.05 to 0.1 mm., being thinnest where they are squeezed between the inner longitudinal muscles. These glands entirely surround the testes and from a definite layer. The two vitelline ducts appear near the median lateral group of glands and pass posteriorly towards the ovary. Here they pass mediad to the ovarian wings, pass dorsally over the ovarian commissure where these two ducts turn medianly, join, and after nearly 0.2 mm. join the fertilization chamber. There are no post-ovarian vitellaria. (Figs. 26, 52.)

The ovary is a very prominent structure, "H" shaped, but with the lower arms longer and slightly narrower than the upper. The formation is follicular, each follicle being connected by a thin stem to the main com-

missure (Fig. 26). This is also characteristic of *C. singularis*, to which it appears related in several other respects. The wings reach within 0.5 mm. of the posterior tip and measure 0.6 to 1.8 mm. long and 0.13 to 0.27 mm. wide, while the commissure has a maximum diameter of 0.23 to 0.27 mm. The oviduct arises at the median posterior edge of the commissure where an inconspicuous oöcapt is formed. The oviduct passes posteriorly for 60 to 75 μ and is joined by the vagina. The fertilization chamber thus formed is about 100 μ long at whose termination the vitelline duct empties and the uterus is formed. Contrary to the usual method of procedure this limb of the uterus passes dorsally and remains in this position until opposite the posterior tips of the ovarian wings. Here the uterus dips ventrally and passes anteriorly; it also becomes surrounded by uterine glands and the cavity becomes somewhat wider. The uterus crosses the ovarian commissure in the middle of the body and becomes more coiled as it passes anteriad. The coils do not pass the posterior limits of the cirrus sac. The last 0.5 mm. of the uterus is lined with a thin layer of circular muscles instead of the usual uterine glands. The eggs are ovoid and are 60 to 68 by 35 to 42 μ, averaging 63 by 38 μ in size.

Pseudolytocestus differtus differs from all of the other species of the subfamily Capingentinae. Both *Capingens singularis* and *Spartoides wardi* have fewer testes, being 210 to 225 and 65 to 105 respectively compared with 725 to 775 in *P. differtus*. The scolex of *C. singularis* and the ovary of *S. wardi* are sufficient characters in themselves to distinguish them from ever being more closely associated than members of the same subfamily. At first glance *P. differtus* appears to belong in the genus Monobothrium. A more careful study shows a number of differences which are valid. First one notes the location of the vitellaria in relation to the inner longitudinal muscles. A glance at the sections show the dearth of longitudinal grooves on the scolex of *P. differtus* with but doubtful indications of the existence of a terminal introvert. Further, every specimen of *M. ingens* examined possessed a cirrus which was extruded thru a bulky annular pad (Fig. 39), while the typical picture of *P. differtus* occurs in figure 52. In only one instance was the cirrus found extruded in the latter species and then the whole outer edge was serrate and not papillate as in Monobothrium. These are sufficient grounds to maintain this form in the new genus Pseudolytocestus. The specific name "*differtus*" was given to indicate the crowded nature of the parenchyma of this parasite.

GENUS SPARTOIDES HUNTER 1929

Generic diagnosis: Capingentinae possessing three pairs of loculi on a distinct scolex. Male and female pores open separately on ventral surface near posterior tip of the last fourth of the body. Cirrus sac opens within the confines of the ovarian wings. One row of main longitudinal

muscles; vitellaria and ovarian follicles are in part cortical to the inner longitudinal muscles; ovarian commissure entirely medullary. Ovary "U" shaped, uterine coils extending anteriorly to the cirrus sac more than twice the length of the ovarian wings. Post-ovarian vitellaria absent. Parasitic in the Catostomidae. Development unknown.

Type and only species: *Spartoides wardi*, Hunter 1929.

This genus was placed in the Capingentinae primarily because of the relation of the vitellaria and ovarian wings to the inner longitudinal muscles. The members of this genus differ from all the others in the shape of the ovary which is like the capital letter "U". This is a marked difference from the characteristic "H" shape of so many of the Caryophyllaeidae, the only other occurring in the genus Caryophyllaeides, Nybelin. This latter genus possesses an ovary with the shape of an inverted capital "A", and is composed of two species, *C. fennica* (Schneider 1902) and *C. skrjabini* (Popoff 1924). In Spartoides the uterine coils extend anteriad to the cirrus sac which has the unique distinction of lying within the ovarian wings at the anterior margin of the ovarian commissure. Further the uterine coils lie almost exclusively anterior to the cirrus sac. The genus was so named because of its great length and thinness thereby resembling a thread.

SPARTOIDES WARDI HUNTER 1929

[Figs. 13, 14, 28, 61–63, 86–89]

1929: *Spartoides wardi* Hunter 1929: 188–189.

Specific diagnosis: With the characters of the genus. Adult parasite 8 to 30 mm. by 0.3 to 0.7 mm. Neck distinct, ranging from 1.6 to 4.7 mm. by 0.2 to 0.55 mm. Maximum body width exclusive of the scolex 0.5 mm. Body oval in cross section; cuticula 2 to 3 μ in thickness; subcuticula and cortical parenchyma indistinguishable, 42 to 58 μ thick. Inner longitudinal muscles present and prominent; outer longitudinal muscles fused with longitudinal cuticular muscles. Testes number 65 to 105, usually appear two per section, and have a maximum diameter of 0.13 to 0.2 mm. Cirrus sac oval to triangular, occupying nearly all of medullary parenchyma; maximum diameter 0.09 to 0.14 mm., circular muscles thin, 9 to 12 μ in width. Seminal vesicle prominent, 0.13 mm. in length, the circular muscles 30 to 45 μ thick. Male and female reproductive systems open on the surface 60 to 85 μ apart. Vagina very short and straight, not forming a receptaculum seminis, but extending dorsally to join the combined ovi and vitelline ducts almost immediately. Vitellaria take their origin in the medullary parenchyma but extend past the inner longitudinal muscles into the cortical parenchyma; smaller than the testes and are 0.1 to 0.15 mm. in maximum diameter. Six pairs of main excretory canals appear in cross section, terminating in typical excretory vesicle. Eggs ovoid 42 to 54 by 22 to 27μ.

Host: *Carpiodes carpio*, Rock and Mississippi Rivers, Illinois and Iowa; *Carpiodes thompsoni*, Lake Pepin (Mississippi River), Minnesota; *Ictiobus cyprinella*, Rock River and Lake Pepin (Mississippi River), Minnesota. In intestine.

Type: Slide No. 29.48 in the collection of Dr. Henry B. Ward.

Paratypes: Slides in the collection of the Department of Zoology University of Minnesota. Slides and vials Nos. 420, 425, 408, 470.1 and 500 in the collection of the author.

The material furnishing the basis for the description of this parasite was taken during the fall of 1924 and the summers of 1925 and 1926. Dr. J. F. Müller collected this form in 1924; Essex and Hunter (1926) gave a general account of the collections of 1925 and the author personally collected many samples of this form while working at the U. S. Fisheries Biological Station at Fairport, Iowa the following year (1926). This parasite was readily distinguishable by its unusual length and thinness which was unique among the forms encountered by the author. Likewise it was collected with greater frequency than many of the other species.

Host	Locality	Collector	Authority
Ictiobus cyprinella (Cuv. and Valenciennes)	Rock River, Sterling, Ill.	J. F. Müller	Hunter (the present paper)
Ictiobus cyprinella (Cuv. and Valenciennes)	Mississippi River, Lake Pepin, Minn.	G. W. Hunter, III and H. E. Essex	Hunter (the present paper)
Carpiod s thompsoni Agassiz	Mississippi River, Lake Pepin, Minn.	G. W. Hunter, III and H. E. Essex	Hunter (the present paper)
Carpiodes carpio (Rafinesque)	Rock River, Sterling, Ill.	J. F. Müller	Hunter (the present paper)
Carpiodes carpio (Rafinesque)	Rock River, Sterling and Rock Falls, Ill.	G. W. Hunter, III and H. E. Essex	Hunter (the present paper)
Carpiodes carpio (Rafinesque)	Mississippi River, Fairport, Ia.	G. W. Hunter, III	Hunter (the present paper)

Spartoides wardi is a very long, thin and narrow parasite; the adults measure 8 to 30 mm. in preserved material while the living specimens reach nearly 50 mm. Usually the adults are from 15 to 50 mm. in length, and the width varies from 0.3 to 0.7 mm. The greatest width appears in the scolex, but in general *S. wardi* presents an unusually monotonous appearance. The neck is long and thin and the vitellaria extend for some distance anteriorly to the testes. The uterine coils and ovary are distinct

while the cirrus sac and seminal vesicle are less sharply defined than usual. The scolex of *S. wardi* is quite prominent and in side view appears wedge shaped (Fig. 13). It varies from 0.2 to 0.54 mm. in length and from 0.5 to 0.67 mm. in breadth. The widest area occurs at the base of the scolex while the distal portion is gently rounded in a typically preserved form. The scolex may take a variety of forms since this organ is very active. Viewing the scolex from the dorsal and ventral surfaces there appear to be two lappets in which are embedded many of the fibers of the inner longitudinal muscles (Fig. 14). These lie between the three weak sucking grooves and may be extended or withdrawn. The action of the scolex is interesting when observed on living material. At rest the scolex appears three pointed or pronged with the median projection extending twice as far anteriorly as the two which flank it. As most of the inner longitudinal muscles are attached to the region between the two side lappets and the central one it keeps the demarkation distinct. The next phase of the movement consists in a drawing in of the median projection and a corresponding bellying out and expansion of the two lateral lappets until all three are of equal size. The last phase is a continuation of the roll of the side lappets until they in turn extend farther anteriorly than the central one. With an extension of the central cone again we have the first position reached. This movement is aided by the flow of the fluid in the excretory canals and particularly the ring clearly seen in figure 62.

In cross section the scolex shows but slight evidences of specialization. The surface is broken on the dorsal and ventral surfaces by three pairs of loculi or bothria (Fig. 61). These are poorly defined and show practically no specialization for adhesion. The inner longitudinal muscles are grouped into eight fasciculi which are connected to each other by scattered fibers; there are from ten to twenty-five fibers in each fasiculus. A few canals of the excretory system can be seen in the more distal portions of the scolex. These are fine and scattered (Fig. 61). As the base of the scolex is approached the inner longitudinal muscles become more definitely separated into eight distinct groups and the irregular collecting ring of the excretory system begins to show clearly (Figs. 62, 89). The two ducts of the ascending canals lie in the medullary parenchyma while outside these appear the wide thin-walled canals of the descending system. The ascending ducts are found to take their origin from those lying next the descending canals of the excretory system in the cortical parenchyma. As the scolex is reached each pair of the canals fuse in the medullary parenchyma to form one (Fig. 62). These may be later reduced; they extend to the more distal portions of the scolex and then turn sharply towards the cortical region where they are absorbed in the collection ring in the lower regions of the scolex. From this ring the six descending canals take their origin. These pass posteriorly and in the lower neck region are joined by

the ascending canals so that the typical paired excretory canals appear in the cortical parenchyma. These descending canals empty posteriorly into the excretory vesicle near the posterior tip of the body. The ascending canals soon pass into the glandular region of the neck after penetrating the medullary parenchyma. The function of these glands is unknown.

The cuticula of this parasite is very thin, measuring from 2 to 3 μ. The cuticula is followed immediately by the thin circular cuticular muscles which are less than 1 μ in thickness. This layer is followed by a clear distinct layer of longitudinal muscles; these probably represent the combined cuticular and outer longitudinal muscle layer as they are more prominent than either of these would be alone. Owing to their position they are considered as cuticular longitudinal muscles (Fig. 63). They have a maximum number of 2 or 3 per fasciculus but usually appear singly, and measure 3 μ in cross sections. The subcuticula, because of the apparent absence of the outer longitudinal muscles, is combined with the cortical layer of the parenchyma. As it varies in thickness from 42 to 58 μ and contains not only the paired ducts of the excretory system but also the nuclei so often confined to the subcuticula.

The male reproductive system is unique in some respects and differs from those heretofore encountered. The testes are large, irregularly ovoid to spherical and measure 0.13 to 0.2 mm. in maximum diameter; they number between 65 and 105. Owing to their size there are but two or more rarely three testes visible in cross section (Fig. 63). Typically one finds a dorsal and ventral testis in section flanked dorso-ventrally by the inner longitudinal muscles and laterally by two or three vitellaria. The testes give rise posteriorly to a small vas deferens situated medianly. This duct expands as the last vitellaria are passed and winds posteriorly keeping ventral to the coils of the uterus (Fig. 28). The path is decidedly tortuous until the ovarian wings are reached when the course of the vas deferens becomes straighter even tho it lies ventrad to the ovarian wings for the greater part of its course (Fig. 28). Soon ofter passing the anterior half of the ovarian wings the vas deferens becomes narrower and more thick walled to form the ductus ejaculatorius. This canal is greatly curved and enters the seminal vesicle near the mid ventral surface (Fig. 88). The seminal vesicle is situated well between the wings of the ovary and in the case of heavily contracted forms it lies beneath the ovarian commissure. (Figs. 28, 88.) This vesicle is larger than the cirrus sac, oval and highly muscular. It is 0.13 mm. long; the circular muscles 27 to 45 μ in thickness, surround a cavity having a diameter of 70 to 75 μ. The seminal vesicle lies dorsal to the cirrus sac and empties into it from above via a short continuation of the ductus ejaculatorius which is 0.06 to 0.12 mm. long and is surrounded by a lining 2 to 3 μ in thickness which in turn is covered by a layer of circular muscles about 12 μ across. The cirrus sac appears roughly triangular in shape and is

surrounded by circular muscles from 9 to 12 μ thick, the maximum diameter of the cirrus sac is from 0.09 to 0.14 mm. It lies ventral to the ovarian commissure and sometimes slightly anterior to it (Figs. 28, 88). The cirrus opens to the outside about 0.5 mm. from the posterior tip of the body. In one case the cirrus was found extruded from the body and measured 45 μ in length by 18 μ in diameter (Fig. 88). The male and female reproductive systems open on the surface 60 to 85 μ apart (Fig. 28).

The female reproductive system has the most unique arrangement yet encountered. The vitellaria are arranged in two lateral rows and so do not surround the testes. They are irregular in shape and are darker and smaller than the testes, measuring 0.1 to 0.14 mm. in diameter. Some of these glands extend past the inner longitudinal muscles as in the case of *Capingens singularis* and *Pseudolytocestus differtus* and so take a more irregular shape than usual (Fig. 63). They are drained by two small vitelline ducts lying mediad to the vitellaria and between them and the testes (Fig. 63). These ducts fuse ventrally to the ovarian commissure to form the common vitelline duct (Fig. 87). There are no post-ovarian vitellaria, the area behind the ovary being filled by the oötype and coils of uterus.

The shape of the ovary is different from any Caryophyllaeidae yet studied, being the shape of a captial "U". It measures 0.4 to 1.2 mm. in length, 0.2 to 0.4 mm. deep and 0.09 to 0.18 mm. broad. Fourth-fifths of the ovary lies anteriorly to the cirrus sac. The follicular ovary lies externally to the inner longitudinal muscles, thus making the follicles cortical rather than medullary as is typically the case. In fact nearly one half of the ovarian wings lie in the cortical parenchyma (Figs. 28, 86). Another peculiarity of this gland lies in the fact that in cross section it appears nearly circular. Ventrally there is a slight break and at the ends a slight lateral turning of the glands which suggests at once the capital Greek letter "Ω" (Fig. 86). The ovarian commissure is quite thick and varies in diameter from 0.13 to 0.18 mm. The oöcapt arises from the median posterior ventral surface of the ovarian commissure. It is fairly well developed, the duct being 8 to 10 μ wide surrounded by muscles on each side to the depth of 8 μ (Fig. 87). In this species the oöcapt gives rise to a short oviduct which has a maximum length of 50 μ before it is joined by the vagina. The oviduct is surrounded throughout its path by a thin layer of circular muscles. The vagina in this species is the shortest yet encountered. It arises as a dorsal continuation of the utero-vaginal canal and its commencement is marked by a small sphincter muscle which occurs at the point of juncture with the uterus (Fig. 87). The vagina extends dorsally for about 0.15 mm. and then turns anteriorly. It joins the oviduct and forms the fertilization chamber, or the vaginal-oviducal canal. This portion is not wider than the vagina proper which has a diameter of 10 to 15 μ. Close to the union of this canal the inconspicuous common vitelline duct empties while the vagina continues almost straight dorsad (Fig. 87). As it reaches the medullary parenchyma it dips

and passes posteriorly to the ovarian commissure entering the oötype proper. Throughout its length the duct is surrounded by a few circular muscle fibers. The oötype is small and the uterus soon leaves the confines of this gland and after several convolutions passes anteriorly dorsal and lateral to the ovarian commissure (Figs. 28, 87, 88). As the ovarian commissure is approached the typical uterine glands appear and are in evidence until within 0.3 mm. or less of the outside. The coils of the uterus are complicated, extending both dorsally and laterally within the confines of the inner longitudinal muscles. When the testes are reached the uterus doubles back upon itself towards the female pore. These coils have a longitudinal extent of between one fourth and one third that of the testicular field; usually about one fourth. Posteriorly the uterus becomes thin walled, passes ventrally to the ovarian commissure and joins the vagina to form the utero-vaginal canal. This is 40 to 60 μ in length and lies but a scant 0.3 mm. from the posterior tip of the body surrounded by a continuation of the cuticula the latter in turn being surrounded by a number of clear cells (Fig. 87). The eggs are ovoid and measure 45 to 54 by 22 to 27μ.

This parasite clearly belongs in the genus Spartoides on the basis of all the characters and as it is the only species so far described there are no comparisons to be made with other forms. From the beginning it is set aside by the peculiar shape of the ovary as well as the arrangement of the reproductive systems. It is named in honor of that great American teacher of parasitology, Dr. Henry B. Ward, head of the Department of Zoology of the University of Illinois.

SUBFAMILY WENYONINA E Hunter 1927

Subfamily diagnosis: Caryophyllaeidae in which the sexual apertures are situated in anterior half of the body. Ovary is situated in posterior body half. Longitudinal muscles may consist of either one thick layer occupying entire cortex or this may be split into two layers resembling those of the Lytocestinae. Vitellaria medullary, confined to two lateral rows. Uterine glands absent.

Type and at present only genus: Wenyonia Woodland, 1923.

GENUS WENYONIA WOODLAND 1923

Generic diagnosis: Wenyoninae in which scolex may or may not be specialized. The longitudinal extent of uterus is at least equal to that of testicular field. Ovary medullary, follicular and "H" shaped. Ovarian commissure not reduced, terminal excretory bladder present. Parasitic in Siluridae. Development unknown.

Type species: *Wenyonia virilis* Woodland, 1923.

To include:

(1) *W. virilis* Woodland 1923.

(2) *W. acuminata* Woodland 1923.

(3) *W. minuata* Woodland 1923.

MORPHOLOGICAL DATA

GROWTH IN LENGTH IN CESTODARIA

It is known that some Cestodarian parasites are less than 0.5 mm. in length when they reach the digestive tract of their definitive host, and that such may grow to be 14 times their original size. In larger species which range from 70 to 80 mm. the increase in size would be 140 to 160 times. The growth appears in the region of the body posterior to and including the first vitellarium. A study has been made of this region of localized growth. The material at hand in several species is remarkably well adapted for such a study, because of the numerous worms, varying in size.

Such regional growth is more readily traced in other groups. The distomes, for example, form an excellent group for such observations. Braun (1894:567) notes that regional growth exists. Von Linstow (1890) working with *Distomum cylindraceum* noted a greater increase in length than width. His data, however, could scarcely be called significant, for he measured only three specimens. Other workers who noted such changes were Thomas (1883) and Leuckart (1886) in *Fasciola hepatica*. Barlow (1923) in measurements of several hundred specimens of *Fasciolopsis buski* finds an interesting though not significant change in proportions. Cort (1921) noted variations in body proportions of *Schistosoma japonicum* which closely parallels the changes described by Manter (1926) for *Otodistomum cestoides*. Ward (1910) notes growth changes for *Azygia sebago*. Here he finds that "The anterior region assumes the form of an elipse surrounding the two suckers. This region changes relatively little in size with growth. In one of the smallest specimens (measuring 1.6 mm.) the distance between the centers of the two suckers was 0.5 mm. In one 10 mm. long, this distance measured 1.0 mm." Mühlschlag (1914) in working on *O. veliporum* found that the ratio between the neck region and the body region was 1:4 in young forms and 1:7.8 in the largest adult. He concludes "dass bei verschiedener Grösse der Tierre der Hinterkörper relativ viel stärker wachst der Vorderkörper."

As far as the writer is able to determine there is no data on growth in length in the Cestodaria. The significance of the initial work in this field may be great, and doubly so if the findings corroborate the results of the workers in other fields. An excellent opportunity was afforded the author for the study of the growth in length upon live Cestodarian material. Specimens were secured from *Carpiodes carpio* in considerable quantities. A microscopic examination of the specimens revealed the presence of the

same species in considerable numbers. The parasites were picked over and identifications made. Measurements of the living material were made and then later made into a table (Table I). By placing the specimens under a cover slip with plenty of water little distortion occurred and they could be measured in an extended condition. Measurements on 26 living specimens were obtained in this fashion. From these parasites which measured from 0.65 to 6.53 mm. several interesting correlations were obtained. Perhaps the most significant is that there is a definite ratio between the distance from the anterior tip of the scolex to the anterior side of the first vitellarium, and from that to the posterior tip of the body. In other words, as the parasite grows in length the portion of the body posterior to the first vitellarium increases more rapidly than the region anterior to it (i. e., the neck). The ratio of the differences increases from 1:1.16 in the specimen 0.65 mm. in length to 1:2.53 in the parasite of over 6.5 mm. This latter one

TABLE I

Measurements of Hypocaryophyllaeus paratarius Based on Live Material

	Total length	Mm. to first vitellarium	Mm. from first vitellarium to posterior tip	Difference in mm.	Ratio
1	0.658 mm.	0.304 mm.	0.354 mm.	0.05 mm.	1:1.16
2	0.845	0.436	0.504	0.098	1:1.24
3	1.132	0.404	0.668	0.204	1:1.43
4	1.467	0.598	0.869	0.271	1:1.45
5	1.868	0.778	1.090	0.312	1:1.40
6	1.888	0.744	1.144	0.400	1:1.55
7	2.112	0.802	1.310	0.508	1:1.63
8	2.124	0.802	1.322	0.520	1:1.64
9	2.342	0.882	1.460	0.578	1:1.65
10	2.549	0.952	1.597	0.645	1:1.67
11	2.668	0.992	1.676	0.684	1:1.68
12	2.945	1.100	1.845	0.745	1:1.67
13	3.042	1.132	1.910	0.778	1:1.68
14	3.125	1.175	1.950	0.775	1:1.69
15	3.327	1.200	2.127	0.927	1:1.77
16	3.499	1.234	2.265	1.031	1:1.83
17	3.522	1.290	2.232	1.042	1:1.80
18	3.666	1.300	2.366	1.066	1:1.82
19	3.922	1.360	2.662	1.302	1:1.95
20	4.200	1.400	2.800	1.400	1:2.00
21	4.529	1.436	3.093	1.657	1:2.15
22	4.720	1.496	3.224	1.828	1:2.22
23	5.000	1.600	3.400	1.800	1:2.12
24	5.520	1.700	3.820	2.120	1:2.24
25	6.014	1.840	4.174	2.334	1:2.27
26	6.536	1.850	4.686	2.836	1:2.53

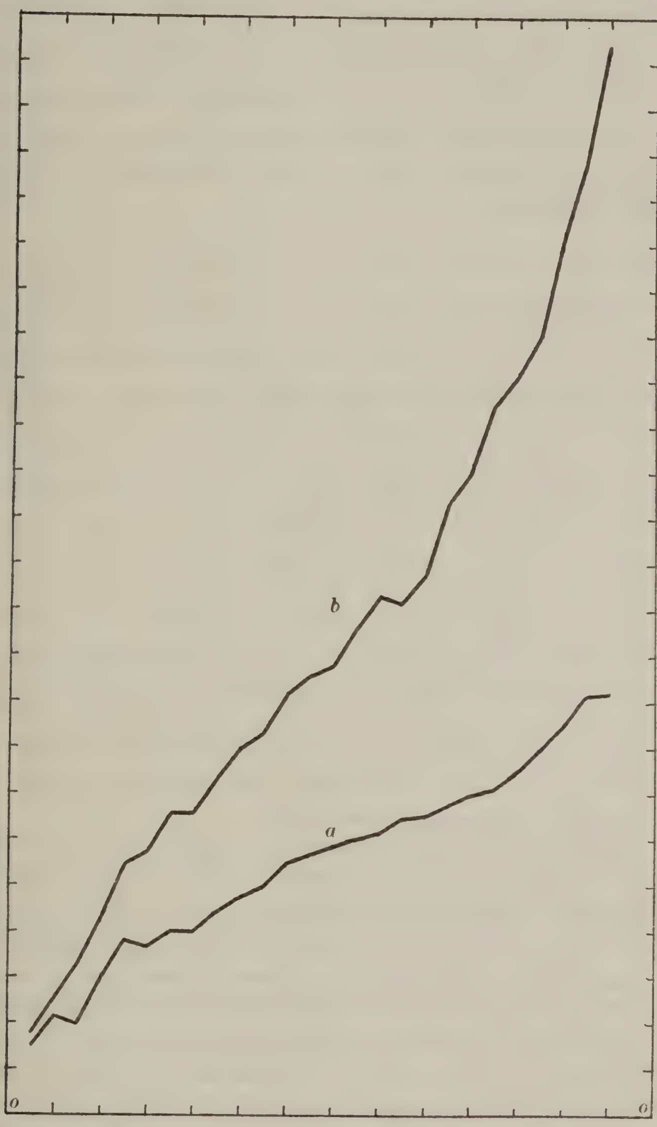

Chart 1. Graphic representation of growth in length in 26 *Hypocaryophyllaeus paratarius*. The base line (0) represents the anterior ends of the parasites while the upper line (b) shows the posterior end of the parasites. The middle line (a) represents the anterior margin of the first vitellarium. Two individuals are indicated between successive vertical lines. Each horizontal line represents two tenths (0.2) of a millimeter.

is sexually mature although the eggs were not present in the uterus in great numbers. This ratio was obtained by dividing the distance to the first vitellarium into the distance from the first vitellarium to the posterior body tip (See Table I). Chart 1 shows this graphically. Here the base line (0) represents the anterior ends of the parasites and the upper curve represents the posterior tip of the body while the middle line marks the anterior edge of the first vitellarium.

GROWTH IN LENGTH IN GLARIDACRIS CONFUSUS

After studying growth in length on living specimens the writer decided to attempt a similar study upon preserved material. The collections were gone over and the vials containing young forms were run into glycerine and those bearing superficial resemblances were then stained and studied again in cedar wood oil. Thus it was possible to eliminate all but one species, and measurements on 106 of this species were taken. In all cases the measurements were made from the distal tip of the scolex to the most anterior vitellarium and from the anterior edge of this to the posterior extremity. In cases of several of the youngest specimens where differentiation had not clearly occurred the distance from the scolex tip to the most anteriad portion of the dark staining-medullary cells, (the anlagen of the vitellaria and testes), was taken. It was found that the total length varied from 0.53 to 20.90 mm. in the 106 individuals. Furthermore, the ratios of the differences ranged from 1:24 up to 1:17.17 in the largest forms studied. This change is of course much more significant than that noted for *H. paratarius* and the study of these data covers more forms and consequently are of greater significance from the statistical standpoint.

After tabulating the measurements an analysis was made of the data and it was found that the parasites fell into seven classes. Class I consists of the individuals whose measurements from the scolex to the first vitellarium were from 0.11 to 0.2 mm., Class II, 0.21 and 0.3 mm., etc. to Class VII, 0.71 mm. and up. Table III shows this very clearly and gives a summary of the data appearing in Table II which includes all of the measurements. Clearly there is a much greater increase in distance from the first vitellarium to the posterior tip than there is from the scolex to the first vitellarium. It should be noted that the maximum measurements in each class show a very definite increase, with the possible exception of Class V. The maximum length for the posterior body portion is only 3.40 mm. while in the preceding class we find it to be 4.44 mm. This is doubtless due to unusual expansion, for the minimum for Class IV is 0.81 mm. compared with 1.23 mm. for Class V, showing a significant increase. The minimum records are perhaps more noteworthy since they probably represent the maximum contraction in each group. Chart 2 gives a graphic representation of these measurements.

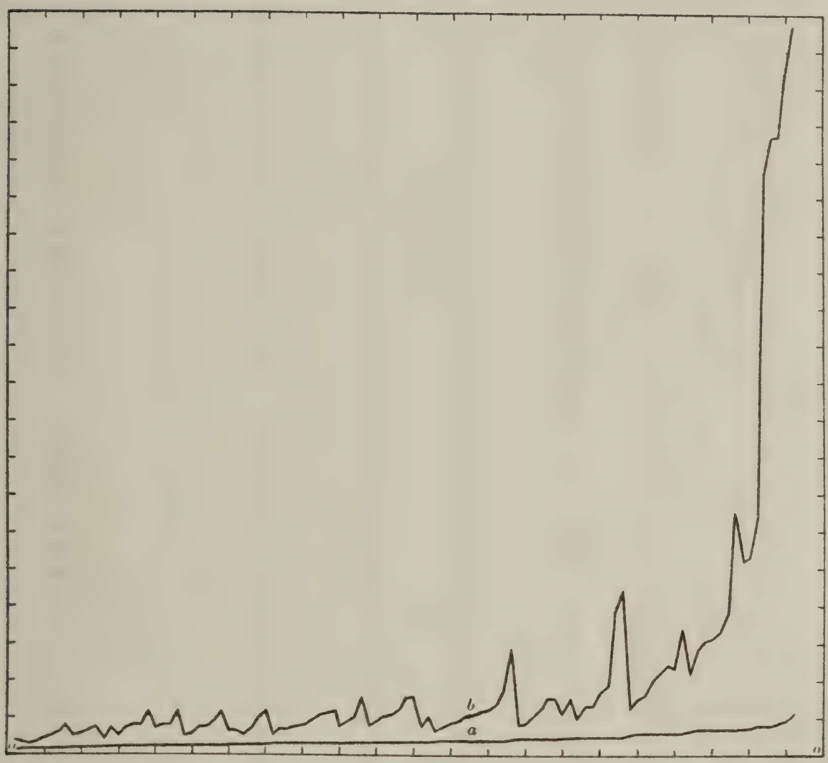

Chart 2. Graphic representation of growth in length in 106 *Glaridacris confusus*. The base line (0) shows the anterior ends of the parasites while the upper line (b) represents their posterior extremities. The middle line (a) indicates the anterior margin of the first vitellarium. Five individuals are represented between successive vertical lines. Each horizontal line indicates one (1) millimeter.

TABLE II

MEASUREMENTS OF 106 GLARIDACRIS CONFUSUS SHOWING VARIATIONS IN LENGTH WITHIN THE DIFFERENT CLASSES

Class	No. Inds.	Distance Scolex to first Vitellarium	Distance first Vitellarium to posterior body tip	Total length
	1	0.12 mm.	0.41 mm.	0.53 mm.
	2	.15	.38	.53
	3	.15	.30	.45
	4	.15	.35	.50
	5	.17	.46	.63
	6	.17	.51	.68
I	7	.17	.61	.78
	8	.17	.81	.98
	9	.18	.51	.69
	10	.18	.56	.74
	11	.18	.66	.84
	12	.18	.76	.94
	13	.20	.41	.61
	14	.20	.76	.96
	15	.22	.51	.73
	16	.22	.76	.98
	17	.22	.81	1.03
	18	.22	.81	1.03
	19	.22	1.13	1.35
	20	.23	.71	.94
	21	.23	.81	1.04
	22	.23	.91	1.14
II	23	.23	1.18	1.41
	24	.25	.51	.76
	25	.25	.58	.83
	26	.25	.74	.99
	27	.25	.76	1.01
	28	.25	.91	1.16
	29	.25	1.13	1.38
	30	.27	.64	.91
	31	.27	.66	.93
	32	.28	.56	.94
	33	.28	.71	.99
	34	.28	1.03	1.31
	35	.28	1.20	1.48
	36	.30	.56	.86
	37	.30	.71	1.01
	38	.30	.71	1.01
	39	.30	.76	1.06
	40	.30	.81	1.11
	41	.30	.96	1.26
	42	.30	1.08	1.38
	43	.30	1.13	1.43
	44	.30	1.18	1.48

TABLE II
(Continued)

Class	No. Inds.	Distance Scolex to first Vitellarium	Distance first Vitellarium to posterior body tip	Total length
	45	0.31 mm.	0.79 mm.	1.10 mm.
	46	.32	.91	1.23
	47	.33	1.03	1.36
	48	.34	1.54	1.88
	49	.35	.79	1.14
	50	.35	.91	1.26
	51	.35	1.05	1.40
	52	.35	1.10	1.45
	53	.35	1.23	1.58
	54	.35	1.54	1.89
III	55	.35	1.59	1.94
	56	.38	.77	1.15
	57	.39	1.06	1.45
	58	.40	.67	1.07
	59	.40	.76	1.16
	60	.40	.82	1.22
	61	.40	.92	1.32
	62	.40	1.04	1.44
	63	.40	1.09	1.49
	64	.40	1.19	1.59
	65	.40	1.24	1.64
	66	.40	1.35	1.75
	67	.40	1.74	2.15
	68	.44	2.85	3.29
	69	.46	.81	1.27
	70	.46	.86	1.32
	71	.46	1.03	1.49
	72	.46	1.28	1.74
	73	.46	1.64	2.10
	74	.46	1.64	2.10
IV	75	.48	1.18	1.66
	76	.49	1.64	2.13
	77	.50	1.04	1.54
	78	.50	1.34	1.84
	79	.50	1.34	1.84
	80	.50	1.70	2.20
	81	.50	1.84	2.35
	82	.50	3.91	4.41
	83	.50	4.44	4.94
	84	.56	1.23	1.79
	85	.60	1.55	2.15
	86	.60	1.60	2.20
V	87	.60	2.07	2.67
	88	.60	2.27	2.87
	89	.60	2.93	3.53

TABLE II
(Continued)

Class	No. Inds.	Distance Scolex to first Vitellarium	Distance first Vitellarium to posterior body tip	Total length
	90	.60 mm.	2.88 mm.	3.48 mm.
	91	.60	3.40	4.00
	92	.66	2.21	2.87
	93	.70	2.88	3.58
	94	.70	3.10	3.80
VI	95	.70	3.15	3.85
	96	.70	3.30	4.00
	97	.70	3.81	4.51
	98	.70	6.50	7.20
	99	0.76	5.25	6.01
	100	.76	5.36	6.12
VII	101	.80	6.41	7.21
	102	.80	15.65	16.46
	103	.81	16.70	17.51
	104	.89	16.72	17.61
	105	.98	18.5	19.48
	106	1.15	19.75	20.90

TABLE III
SUMMARY OF MEASUREMENTS ON GROWTH IN LENGTH IN GLARIDACRIS CONFUSUS

Class	No. Inds.	Distance Scolex to first Vitellarium	Distance first Vitellarium to posterior extremity	Total Min. Max.
I	14	0.12–0.2 mm.	0.3 –0.81 mm.	0.45–0.98 mm.
II	30	0.22–0.3 mm.	0.51–1.20 mm.	0.73–1.48 mm.
III	23	0.31–0.4 mm.	0.67–1.74 mm.	1.07–2.15 mm.
IV	16	0.46–0.5 mm.	0.81–4.44 mm.	1.27–4.94 mm.
V	8	0.56–0.6 mm.	1.23–3.40 mm.	1.79–4.00 mm.
VI	7	0.66–0.7 mm.	2.21–6.50 mm.	2.87–7.20 mm.
VII	8	0.76–up	5.25–19.75 mm.	6.01–20.90 mm.

The matter of growth in length has several interesting angles. In the first place it brings the Cestodaria in line with the trematodes to the extent of showing that the greatest development in both groups occurs in the posterior body region and back of a definite organ. The author does not intend to intimate that any homology exists between these two groups, but simply an analagous type of growth. Even more striking is the comparison with the cestodes. Here are two types of individuals essentially similar, both possessing a scolex, undifferentiated neck, and the body proper containing

the reproductive organs. In the cestodes it is a well known fact that the region of growth lies at the neck and that proglottids are budded off posteriorly with the oldest proglottid lying at the distal extremity. Do we not have evidence of an essentially identical phenomenon here? The region of growth lies, to all intents and purposes, in the neck, for it is this region, and the portion of the body just posterior to it, which shows the greatest changes. The measurements of the length of scolices and necks do not change materially between the young and adult stages, but the body measurements do change corresponding to the proglottids of the cestodes, and the bulk of the growth occurs in this region. This is particularly true of some of the Pseudophyllideans. *Clestobothrium crassiceps* and *Abothrium crassum*, for example, both show this well, as do other forms. In the case of *A. crassum* a young plerocercoid larva, measuring slightly over 0.5 mm. in length had a scolex between 0.025 and 0.03 mm. long, while an older strobila with a length of nearly 3 mm. had a scolex measuring the same or less than that of the plerocercoid just over 0.5 mm. in length. This example serves to show that these, as the Cestodaria, do not undergo any appreciable increase of scolex length. In both these groups the neck does not show any remarkable differences of changes in proportion. This difficulty in measuring neck distances in plerocercoid larvae of the Pseudophyllidea lies in the fact that in the earliest forms differentiation does not occur. *A. crassum*, however, may once again serve as an example. Here the neck, as determined by the distance from the base of the scolex to the first proglottid, varies between 0.2 and 0.4 mm. in specimens which range in size from slightly under 2 mm. to over 8 mm. It is evident therefore, since this species reaches a maximum length of 870 mm. (Cooper 1919:187) that the bulk of the growth occurs posterior to the neck region. In other words the regions which contain the reproductive organs in both the Pseudophyllidea and the Cestodaria are the localities which show the greatest growth. It is evident that the neck region in the Cestodaria as in the cestodes is the region of growth.

The data on growth in length is of further significance in that it points to the danger of basing data on incomplete measurements. For unless minimum and maximum length measurements, etc. are made it may be possible to confuse species. And, whenever possible, the measurements of organs, organ systems, etc. should include minimum and maximum measurements based upon as many different individuals as are available.

LIFE HISTORY STUDIES

The original purpose of this monograph was to elucidate the life history of various Cestodaria. Some work had been done in the past by a few European workers. A survey of the literature reveals that the generally accepted theory concerning the life history of the Caryophyllaeidae is essentially as follows: The egg or larva reaches the digestive tract of a

Tubificid worm and then bores through to the body cavity. At this stage it may possess a caudal vesicle (like *Archigetes sieboldi*). After undergoing a certain amount of development the worm is eaten by the definitive host (a fish); upon reaching the digestive tract of the fish the caudal vesicle of the parasite is lost and it becomes sexually mature. D'Udekem (1855) was the first to find such a "larval form" in *Tubifex rivulorum* and *Nais proboscoidea.* According to Nybelin (1922) this form resembles the scolex of *C. laticeps* rather closely. Two other forms also possess marked resemblances to this parasite, Ratzel's (1868) "*C. appendiculatus*" from the genital region of *Tubifex tubifex* and Mrázek's (1901) specimen from the same genus, Tubifex. This latter larval form was described by him as the larval stage of *C. laticeps* (=*C. mutabilis*). It possessed the characteristic "Fäserzellenstränge" of *C. laticeps* as well as some other morphological features. Mrázek therefore claimed this was the larval form and stressed the common possession of the "Fäserzellenstränge." This point unfortunately loses much of its significance when one realizes that there are at least three other species possessing these same characteristic tissues. Leuckart in the meantime (1878) had described *Archigetes sieboldi* from the Tubifex. This is considered by Lühe (1910) as a synonym of *A. appendiculatus.* Nybelin (1922) shows that *A. sieboldi* is the proper cognomen and therefore records *A. appendiculatus* as the synonym and points out that the original "*C. appendiculatus*" of Ratzel (1868) was probably a larval stage of *C. laticeps* as noted by Leuckart (1869). In 1908 Mrázek described a new and valid member of the genus, *A. brachyurus.* This form was easily distinguished by a shorter caudal vesicle and other morphological differences. Wisniewski (1928) describes a new member of this group, *A. cryptobothrius.* Ward (1911) records the presence of a Cestodarian from a fish. According to this preliminary note the parasite possessed some of the characters of both Caryophyllaeus and Archigetes.

Thanks to the kindness of Professor Frank Smith the author came into the possession of several parasitized Tubificid worms. These clearly belonged to the genus Archigetes and will be described in detail when more material is available. The author resolved to test out the hypotheses on the life history of the Cestodaria. Altho the results are negative the experiments will be outlined in the hope that it will prove an aid to other workers. Besides the theory of infection outlined in the preceding paragraphs which has been supported by various European workers the author wondered if there might not be some other explanation. It seemed more logical to assume that the eggs of all species except Archigetes were eaten by some Entomostracan and that after a developmental period had elapsed these in turn were eaten by a fish. This suggested cycle is similar to that worked out for other tapeworms [cf Janicki and Rosen (1917), Rosen (1918, 1919), Meggitt (1924), Hunter (1928, 1929) and Essex (1928, 1928a)]. A study of the contribu-

tions on the food of the hosts of the Caryophyllaeidae in North America clearly shows a predominance of Entomostraca over Tubificidae [see Forbes and Richardson (1908), Pearse (1918, 1921) and the reports of Greeley and Sibley of the New York State Department of Conservation on the Genesse and Oswego watersheds (1927 and 1928)]. Again the parasites have been found in numbers in the intestines, sometimes as many as several hundred in a single host. This is not significant in itself, but when coupled with the fact that in a study of over 5,000 Tubificidae from various localities less than 1 percent showed infection with Cestodaria it clearly indicates that great numbers of these worms must be eaten if they are to acquire several hundred parasites (all of which were in the same stage of development). Surely then is it not peculiar that these worms have not been recorded as constituting a more significant part of the diet of the fish?

The author decided to test the latter part of this theory by securing evidence on the rate of dissolution of Tubificidae in the stomachs of various hosts. Three species of fish were used, *Carpiodes carpio*, *Ictiobus cyprinella* and *I. bubalus*, in all 14 fish. Representatives of both the genera Limnodrilus and Tubifex were used in the experiments. The stomachs of the fish were asepticly opened and a worm placed therein. The Tubificidae were soon killed; the time required ranging from 3 minutes and 15 seconds to 10 minutes and 30 seconds. Complete dissolution occurred from 27 minutes and 35 seconds to 6 hours 25 minutes and 15 seconds (Table IV). Many of the fish used for stomach examinations are not killed immediately. Thus it is readily conceivable how the acid of the fish stomach would soon kill the

TABLE IV

Rate of Dissolution of Tubificidae in Fish Stomachs

Fish	Tubificidae	Dead in			Dissolved in		
		Hr.	Min.	Sec.	Hr.	Min.	Sec.
Carpiodes carpio	Limnodrilus sp.	0	8	30	6	25	15
C. carpio	Limnodrilus sp.	0	3	15	6	20	10
C. carpio	Limnodrilus sp.	0	3	20	6	12	15
C. carpio	Tubifex sp.	0	4	10	6	10	25
C. carpio	Tubifex sp.	0	10	30	4	5	10
C. carpio	Tubifex sp.	0	6	15	0	35	39
Ictiobus cyprinella	Limnodrilus sp.	0	8	45	4	46	5
I. cyprinella	Limnodrilus sp.	0	6	13	2	12	10
I. cyprinella	Tubifex sp.	0	6	00	0	27	35
I. cyprinella	Tubifex sp.	0	4	20	1	23	10
Ictiobus bubalus	Limnodrilus sp.	0	6	15	4	1	00
I. bubalus	Limnodrilus sp.	0	3	15	0	39	10
I. bubalus	Tubifex sp.	0	3	25	3	25	25
I. bubalus	Tubifex sp.	0	5	30	4	45	15

worm. It is but a step further to visualize the rapid disappearance of these worms by the grinding action of the muscular walls of the stomach aided by the presence of a few grains of sand or foreign matter. This would explain how the Tubificidae have but seldom been reported as food. Such an explanation leaves out of consideration the fact that in some cases at least the minute setae of these worms would have been noted, even tho the examination were rather cursory.

The existence or non-existence of operculate eggs amongst the Caryophyllaeidae is also a point worth investigating. This is very difficult to determine unless fresh material is available. Cooper (1920) reported that *Glaridacris catostomi* possessed operculate eggs. This means that there is some sort of a free swimming larval stage and that the first intermediate host might be actively sought out by the parasite, or devoured as a choice morsel by the host.

Some of the other experiments which were tried but failed to bring results will be briefly noted. Tubificidae from the Illinois River were carried to the U. S. Biological Fisheries Station at Fairport, Iowa, where infection experiments were attempted. Artificial inoculation per anus and mouth were tried without success. Likewise fish were planted in back waters, or sloughs, which had lost their connection with the Mississippi River. Such fish had been yielding 100 percent infection with young stages. Tubificid worms were not present and routine examinations of other possible intermediate hosts were negative. A period of high water re-established connection with the river and invalidated any results. Successful infection would have been significant since the Tubificid worms were absent.

Wisniewski (1928) has worked out experimentally the life cycle of his new species, *A. cryptobothrius*. He finds that this form possesses only one host, *Limnodrilus hoffmeisteri*. He secured positive infection in six of seven attempts and notes that the early stages of development may be encountered in different parts of the host, there being no special region where they occur when immature. The complete paper of Wisniewski will undoubtedly give the details of this interesting piece of work.

AFFINITIES OF THE CARYOPHYLLAEIDAE

Wisniewski (1928) follows his description of *A. cryptobothrius* with a brief account of some experiments on the life cycle of this form. He experimentally infected *L. hoffmeisteri* and found that as in the case of *A. seiboldi* there is but the one host, a Tubificid worm. As he points out there is no theoretical nor experimental grounds to longer assume that Archigetes may be a paedogenetic larval form of Caryophyllaeus. It does not preclude, however, so far as the evidence goes, the possibility of a similar Archigetes-like larva passing an embryonic period in the body cavity of Tubificid worms. However, it does seem extremely unlikely that this will prove to be

the case. It appears more probable that such forms as noted by D'Udekem, Ratzel and Mrázek and called Caryophyllaeus larvae by Nybelin (1922) and others will prove to be immature members of the genus Archigetes.

The question of the phylogenetic relationships of this group has been briefly touched previously. Wisniewski (1928) feels that he has sufficient evidence upon which to base his conclusion that the genus Archigetes represents a neotaenic procercoid larva of a Bothriocephalid tapeworm. To me it appears that to date our knowledge of the ontogeny of the related genera both in the Bothriocephalidae as well as the remainder of the Caryophyllaeidae is insufficient to warrant such conclusions. As pointed out earlier in the discussion we must wait until we secure a more detailed knowledge of the life histories of the members of these two groups until we can accurately determine their phylogenetic relationships. We are amassing evidence at a rapid pace for already we have considerable morphological evidence of apparent identities in structure between the groups. Nybelin (1922) realized this and attention has previously been called to such interesting forms as *Capingens singularis*, a cross section of whose scolex might readily be mistaken for one of the Bothriocephalids (Fig. 11). Likewise there are remarkably accurate reproductions in nature of the acetabular type of sucker (Figs. 16, 17), while Wisniewski (1928) has pointed to certain Bothriocephalid characteristics of his new form, *A. cryptobothrius*. In addition he suggests that the development of this species represents a neotenic Bothriocephalid procercoid larva. Certain points come to my mind, as the possession of a caudal vesicle bearing six embryonic hooks, the equivalent perhaps of the cercomer noted on all Bothriocephalid procercoids studied up to the present time. But what evidence do we have that this, as well as as the other similarities noted above, is not a case of convergence? Light will perhaps be thrown on this point when Wisniewski's completed paper appears. Until that time criticism is unjustified.

Ward (1911) discusses a parasite belonging to the Caryophyllaeidae from the intestine of fishes from the Illinois River. These resembled both the genus Caryophyllaeus and Archigetes, the former in the type of host and absence of a caudal vesicle and the latter in organization. This led Ward to two alternative hypotheses. In the first he suggests that the European form might have an undiscovered adult stage in some vertebrate host. In such a case the caudal vesicle would be lost as in Caryophyllaeus and the form he found. This possibility has been destroyed by Leuckart's and more recently Wisniewski's experiments, particularly the latter's in which he completes the life cycle of *A. cryptobothrius* and finds that it is confined to a single invertebrate host. Ward's second hypothesis is that the form noted by him may represent a higher stage in development. In such a case the European form would be a degenerate type which has lost the intermediate stage. Support for this conjecture is found in Pintner's interpreta-

tion of Amphilina as well as Woodland's work on this Cestodarian. Pintner (1903) claims that the location of Amphilina in the body cavity is evidence for this interpretation. Or as Ward suggests, the form described by him may indicate an adaptation whereby the invertebrate parasite has acquired a vertebrate host. The writer feels, however, that altho the suggestions are interesting the life history of all of the Caryophyllaeidae except Archigetes will prove to be somewhat similar to that of the other cestodes and will include an Entomostracan. Evidence for this view lies in the food of the hosts of these parasites which is largely Entomostracan. One other possibility remains and that is that direct infection occurs in the remainder of the Caryophyllaeidae as in Archigetes. All of the hosts both here and abroad are found amongst the Siluridae, Catostomidae or Cyprinidae, and all of these feed on or near the bottom and so might secure infection accidentally.

As for the remainder of the Caryophyllaeidae and the family as a whole but few words need be added. Nybelin (1922) in his excellent monograph on the Pseudophyllidea discusses the situation thoroly. He creates a new family, the Cyathocephalidae, to hold the Caryophyllaeidae of Leuckart and the Cyathocephalinae of Lühe. This is characterized as follows:

"Pseudophyllideen mit anapolytischer und acraspeder Strobila. Geschlechtsöffnungen flächenständig, median, die desselben Genitalkomplexes stets auf derselben Fläche der Strobila; Mündung des Uterus zwischen denen des Cirrus und der Vagina, in innigster Beziehung zur letzteren. Germarium median gelegen, ausgesprochen zweiflügelig mit lobierten Flügeln; das Gewebe der Seitenflügel viel kompakter als das der Querbrücke. Oötyp von gut ausgebildeten "Schalendrüsen" umgeben. Uterus gewunden, ohne lokale Erweiterung und mit echter Öffnung. Uterinaldrüsen gut ausgebildet. Eier dickschalig, gedeckelt. Geschlechtsreif in Fischen (Ausnahme Archigetes)."

The Caryophyllaeidae might well remain as a subfamily as created by Nybelin except that the characters indicated by him deal with features which are in part of less than subfamily and in part of more than subfamily importance. Furthermore the situation has been immensely complicated during the past few years by the quantity of new forms which have been described and with characters as narrow as those noted for his subfamily (see page 14). Earlier it was pointed out that Woodland (1923, 1926) went to the opposite extreme and deleted many valid genera. Granting that classification is entirely pragmatic it is equally evident that a system is needed which expresses the relationships within the family as clearly as possible as well as the interrelationships of the group. As noted in previous publications (Hunter 1927, 1929) the subfamily Caryophyllaeinae of Nybelin was taken out of the Cyathocephalidae and placed as an independent family of the Pseudophyllidea. This was given the diagnostic characters noted on

page 28 and was in turn subdivided into three subfamilies, the first of these, the Caryophyllaeinae, being modified from Nybelin's characterization of it. The Cyathocephalidae, the second family of the Pseudophyllidea and a close kin of the first, would then be composed of but a single family which might well be characterized by the following:

CYATHOCEPHALIDAE NYBELIN 1922
(=Cyathocephalinae Lühe) Char. emend.

Family diagnosis: Pseudophyllideans with stumpy strobila bearing but few proglottids. Poorly developed scolex and organs of attachment at anterior end. Reproductive system opens medianly, being multiply arranged one to each proglottid. Testes in two lateral fields, the larger part outside the longitudinal nerve strand. Vas deferens without external seminal vesicle; ductus ejaculatorius with distinct wall. Ovary bilobed; uterus and vagina open into common utero-vaginal canal guarded by a sphincter muscle. Vagina forms distinct receptaculum seminis and sharply set off ductus seminalis. Vitellaria annularly arranged up to median part of the proglottid. Eggs very small. Adult in intestine of fishes.

Such an arrangement has the advantage of keeping the Cyathocephalidae and Caryophyllaeidae on an equal footing and yet not so intimately associated as they would be were they in the same family. This appears more satisfactory since in reality a deep gulf exists between the two groups as is evidenced by the differences in strobilization, the Caryophyllaeidae being entirely monozooic while the Cyathocephalidae are polyzooic. Furthermore there may be a significant difference in the life history of these two groups, certainly there is evidence of this possibility as far as Archigetes is concerned, and it may prove to be true with the other genera of the family. In addition there are several clearly defined morphological differences such as the sphincter about the mouth of the utero-vaginal canal, the multiplication of the reproductive organs, the position of the testes in relation to the inner longitudinal muscles and the nerve strands. Clearly then there appear ample grounds for the separation of these two groups, the Caryophyllyaeinae and Cyathocephalinae and their elevation to the rank of separate and equal families, the Caryophyllaeidae and Cyathocephalidae respectively.

PATHOLOGICAL EFFECT OF CESTODARIAN INFECTION

The Cestodaria are for the most part harmless parasites which have but little effect upon their host. They are typically free in the intestines but a few appear to have some pathological significance. Linton (1893) was the first to record any pathogenicity, citing *C. terebrans* which he found in pits in the mucosa where several individuals were crowded into a single pit. Altho this pit received but passing attention one cannot help but realize

that a number of these might constitute a serious obstruction in the alimentary canal. Cooper (1920) described and figured similar mucosal pits. These he described as follows:

"... but many larvae—forty-one in the case of the third fish in the table—were attached to the bottoms of deep pits in the mucosa of the pyloric region of the stomach. These pits were not mere depressions of the wall of the stomach but actual cavities .... bordered by a pronounced annular thickening of the mucous membrane and as much as 2 mm. in diameter. Larvae ranging in size from almost the smallest met with to those near the adult stage in development were tightly crowded into these pits and at the same time strongly contracted longitudinally."

According to the figure shown in connection with this description one gains the impression that there is considerable proliferation of tissue.

More recently Bovien (1926) has described a very interesting situation in a catfish, *Clarias batrachus*. Here the parasite, *Djombangia penetrans*, bores its way through the muscular layers of the intestine carrying with it tissue from the submucosa. As Bovien points out this may have a detrimental effect since a simple bursting of this capsule places the body cavity in communication with the digestive tract. It appears to me to be the most important of any reported to date.

During the course of my collections only one form has been found which shows similar tendencies. This is *Monobothrium ingens*. It was found that from 1 to 7 adults might be present in a single pit. The smallest pit encountered measured 5 by 8 by 6 mm. in depth. The largest was 11 by 13 by 8 mm. These extruded into the intestine more than into the body cavity and in one instance two nearly closed the intestine. In every case the scolex of the parasite was found embedded in this proliferating tissue. This phenomenon suggests the possibility that the cells of uncertain function described in the neck of this and other Cestodaria may be glandular in nature and so secrete some substance which aids the parasite in its boring into its host. These cells may pass their products into small ducts which in turn lead to the exterior in this part of the scolex, or neck. Further evidence for the support of this theory lies in the fact that in case penetration of the tissues is not accomplished, abnormal growth of tissue appears instead. This explanaation is further substantiated by the presence of similar groups of cells in the neck of *C. terebrans*, *G. catostomi*, and also in *G. hexacotyle*. In the case of the latter no information concerning its pathogenicity is available.

These four parasites, *C. terebrans*, *G. catostomi*, *D. penetrans* and *M. ingens* are the only Caryophyllaeidae known to have a pathogenic effect upon their host. In every case the injury appears to be of a mechanical nature. In *C. terebrans* the parasite is poorly equipped for such work since the scolex is unarmed. In *G. catostomi* the scolex has three pairs of loculi while in *M. ingens* which causes a more severe injury, the scolex is armed with 6 weak loculi and a terminal introvert. That there is actually any correlation

TABLE V. DISTRIBUTION OF CARYOPHYLLAEIDAE ACCORDING TO CONTINENTS

Continent	Subfamily	Genus	Species
North America	Caryophyllaeinae	Caryophyllaeus	*C. terebrans*
	"	Glaridacris	*G. catostomi*
	"	"	*G. hexacotyle*
	"	"	*G. laruei*
	"	"	*G. confusus*
	"	Monobothrium	*M. ingens*
	"	Biacetabulum	*B. infrequens*
	"	"	*B. meridianum*
	"	"	*B. giganteum*
	"	Hypocaryophyllaeus	*H. paratarius*
	Capingentinae	Pseudolytocestus	*P. differtus*
	"	Capingens	*C. singularis*
	"	Spartoides	*S. wardi*
Europe	Caryophyllaeinae	Caryophyllaeus	*C. laticeps*
	"	"	*C. caspicus*
	"	"	*C. fimbriceps*
	"	Monobothrium	*M. wageneri*
	"	Caryophyllaeides	*C. fennica*
	"	"	*C. skrajabini*
	"	Archigetes	*A. sieboldi*
	"	"	*A. brachyurus*
	"	"	*A. cryptobothrius*
Africa	Lytocestinae	Lytocestus	*L. filiformis*
	"	"	*L. chalmersius* (?)
	"	Monobothroides	*M. cunningtoni*
	"	Lytocestoides	*L. tanganyikae*
	Wenyoninae	Wenyonia	*W. virilis*
	"	"	*W. acuminata*
	"	"	*W. minuata*
Asia	Caryophyllaeinae	Caryophyllaeus	*C. syrdarjensis*
	"	"	*C. armeniacus*
	"	"	*C. gotoi*
	Lytocestinae	Lytocestus	*L. adhaerens*
Java	Lytocestinae	Djombangia	*D. penetrans*
	Caryophyllaeinae	Caryophyllaeus	*C. javanicus*
	"	"	*C. oxcycephalus*
	"	"	*C. serialis*
	"	"	*C. tenuicollis*
	"	"	*C. microcephalus*
	"	"	*C. aculus*
Australia	Lytocestinae	Balanotaenia	*B. bancrofti*

between the type of scolex and the mucosal pit is improbable but the situation is none the less interesting. It should be borne in mind that actual penetration of the intestine itself cannot be so difficult since young larvae of a number of parasites regularly reach the body cavity of their host in this manner. *Proteocephalus amblopiitis* larvae do this in the second intermediate host when armed only with an invaginated scolex without hooks (Hunter 1928) and other examples may be found. Bovien cites *D. penetrans* and Marochina (1925) tells of the pathogenic effects of five intestinal parasites.

DISTRIBUTION OF CARYOPHYLLAEIDAE

The accompanying table lists the subfamilies, genera and species of the Caryophyllaeidae which are found on each continent. An examination of Table V shows that there are thirteen species recorded from North America. These fall into eight genera and two subfamilies; Europe follows with nine species, four genera and one subfamily; Africa is next with seven species, four genera and two subfamilies, while Java has seven species, two genera and two subfamilies. It is probable that this will be reduced to one subfamily when the material is re-examined. If Java is included with Asia, as it was in prehistoric times, the total for Asia would be eleven species, three genera and two subfamilies. Asia follows with four species, two genera, and two subfamilies, and Australia trails with one species. No species of this group have been reported from South America, probably because but little parasitological work has been done on the proper hosts on these continents. Nor are there any records from Great Britain, the East or West Indies, Iceland or Greenland.

The records are too meager to justify any broad conclusions as to the distribution of these Cestodaria over the larger land areas. One might expect to find the same species on different continents. This was found in the case of *Proteocephalus macrocephalus* (La Rue 1914). It is significant that genera have been reported from more than one continent. The genus Caryophyllaeus occurs in Europe, Asia, and North America. Monobothrium is likewise reported from Europe and North America while Lytocestus is present in Asia and Africa. Indeed it is probable that as investigations of fish parasites are carried on the distribution of the genera will be materially increased, and it is quite possible that identical species may be reported from the different continents.

FISH HARBORING TWO OR MORE SPECIES OF CARYOPHYLLAEIDAE

The accompanying table indicates that eight species of fish are known to harbor two or more species of the Caryophyllaeidae. These six species fall into three families, the Cyprinidae, Catostomidae and Siluridae (Table VI).

TABLE VI. FISH HARBORING MORE THAN ONE SPECIES OF CARYOPHYLLAEIDAE

Host	Species of Caryophyllaeidae Harbored	Distribution of Parasite
Abramis brama	*Caryophyllaeus laticeps*	Sweden; Don River, Russia
	Caryophyllaeus skrjabini	Don River, Russia
	Caryophyllaeus caspicus	Near Caspian Sea, Russia
Cyprinus carpio	*Caryophyllaeus laticeps*	Europe and Africa
	Caryophyllaeus fimbriceps	Near Caspian Sea, Russia
Catostomus commersonii	*Glaridacris catostomi*	Douglas Lake, Mich. Burntside Lake, Minn.; Lake Erie, N. Y.
	Glaridacris laruei	Green Lake, Wisc.; Lake Mendota, Wisc.; Douglas Lake, Mich.
Carpiodes carpio	*Hypocaryophyllaeus paratarius*	Rock River, Ill.
	Capingens singularis	Rock River, Ill.
	Spartoides wardi	Rock River, Ill.
Ictiobus bubalus	*Caryophyllaeus terebrans*	Tallahatchie River, Miss.
	Glaridacris confusus	Mississippi River, Ia.
	Pseudolytocestus differtus	Tallahatchie River, Miss.
Ictiobus cyprinella	*Monobothrium ingens*	Mississippi River, Minn.
	Hypocaryophyllaeus paratarius	Mississippi River, Ia.
	Spartoides wardi	Mississippi River, Minn.; Rock River, Ill.
Clarias batrachus	*Lytocestus indicus*	Nagpur, India
	Djombangia penetrans	Djombang, Java
	Caryophyllaeus javanicus	Djombang, Java
	Caryophyllaeus oxycephalus	Djombang, Java
	Caryophyllaeus serialis	Djombang, Java
	Caryophyllaeus tenuicollis	Djombang, Java
	Caryophyllaeus microcephalus	Djombang, Java
	Caryophyllaeus acutus	Djombang, Java
Macrones nigriceps	*Caryophyllaeus microcephalus*	Djombang, Java
	Caryophyllaeus acutus	Djombang, Java

It is interesting to note that one of the species is the German carp, *Cyprinus carpio*. This fish was introduced into this country in 1877 according to Forbes and Richardson (1908).* Essex and Hunter (1926) report that

* De Kay places the date of the introduction of the German carp, *Cyprinus carpio*, into New York State, at 1831 (Smallwood and Smallwood, 1929). The Smallwoods furnish additional data on the scarcity of parasites in this fish.

"In Europe von Linstow and Lühe list sixteen helminths found in this fish: one nematode (larval stage), two Acanthocephala, eleven trematodes and two Cestodaria." Since then another Cestodarian parasite, *C. fimbriceps*, has been found in this same fish. Essex and Hunter (1926) examined 26 *Cyprinus carpio* but only found five parasitized, one with nematodes and four with Acanthocephala. None of the 26 harbored Cestodaria. Since the collection of those data this author examined thirteen more *C. carpio* and never found a Cestodarian parasite. The situation is interesting to say the least. Presumably the feeding habits of the European and American *Cyprinus carpio* are essentially the same. The dearth of Cestodarian and other parasites must lie then in the inability of the European forms to become established over here. This is more readily understood when one goes into the history of the introduction of these carp into this country (Essex and Hunter 1926: 154). The adult *C. carpio* were brought to Washington, D. C. in 1877 and bred in fish ponds. The young fish were then distributed to twenty-five states. It is evident that the life cycles of the parasites must have been broken and that the only parasites which the introduced carp has now are those which it has picked up in its new environment.

An analysis of these eight cases of multiple infection shows that in *Abramis brama* and *Cyprinus carpio* the different species occur on the same continent, but in widely separated localities, while in the other hosts there is some overlapping of regions. Thus *Ictiobus bubalus* taken from the same stream (Tallahatchie) harbors two different genera of parasites and a third from the same host from another connected river (the Mississippi) some distance away. Again *I. cyprinella* yields two distinct genera from the same locality and further down the river (Mississippi) it harbors a third. Still more striking is the case of *Carpiodes carpio* which sheltered three distinct genera and species from the same river (Rock). Upon the other hand *Catostomus commersonii* harbored two species from five widely scattered lakes, one of the lakes (Douglas Lake, Michigan) yielding both species. One of the most interesting hosts is the Silurid *Clarius batrachus* which harbors eight species and three genera from Asia and Java. To be sure, the generic number will undoubtedly be reduced upon further study since even the incomplete description given by Bovien (1926) shows characters which resemble those of the genus Lytocestus. Two genera come from Java and one from India. One other host from Java, *Macrones nigriceps* harbored two species from the same genus which also occured in *Clarias batrachus*.

CARYOPHYLLAEIDAE OCCURRING IN TWO OR MORE SPECIES OF FISH

Eleven species of Caryophyllaeidae have been found to occur in more than one species of fish. These species are listed and are indicated by an asterisk (*) in appended Table VII which gives a summary of the parasites and the distribution for all species. These species are *Caryophyllaeus laticeps*, *C. caspicus*, *C. terebrans*, *Glaridacris confusus*, *Caryophyllaeides fennica*, *Hypocaryophyllaeus paratarius*, *Biacetabulum giganteum*, *Capingens singularis*, *Spartoides wardi*, *Caryophyllaeus microcephalus* and *C. acutus*. As many of the hosts as possible have been carefully examined in the hope that some evidence might be adduced to indicate the relations existing between the parasite and its host.

Caryophyllaeus laticeps

Nybelin (1922) reports finding specimens of this species in *Abramis brama* from the fish market in Upsala, Sweden, on September 6, 1917 and May 29, 1918. Popoff (1924) reports 30% infection of this same species taken from the same host from the delta of the River Don in 1918. In the case of the hosts the former was undoubtedly caught somewhere in Sweden, possibly from some of the lakes and streams near Upsala, while the latter was taken from the waters flowing into the Black Sea by way of the Sea of Azov, two localities widely separated. This suggests a wide distribution of this form and that an examination of the host from other locations may lead to additional geographical records. The general distribution of the German carp, *Cyprinus carpio* throughout Europe explains to some extent the wide distribution of this parasite as evidenced by the records of this host. Lühe (1910) lists 22 species of fish which harbor this parasite. Undoubtedly there has been some confusion and further study may reveal new species. Baylis (1928) adds another host, *Barbas tropidolepis*, from Lake Tanganyika, Africa.

Caryophyllaeus caspicus

According to the account of Miss Klopina this worm was present in two genera and three species of fish, *Abramis brama*, *A. sopa*, and *Vimbra vimbra*. These hosts were examined by members of the Caspian Expedition of 1914–1915. No definite records as to the location of the hosts were available in the original article other than has been indicated above. However, it is probable that collections were made at the mouths of the major rivers (as the Volga, Ural, Emba, Kuma and Terek Rivers) emptying into the Caspian Sea.

Caryophyllaeus terebrans

Heart Lake in the southeastern corner of Yellowstone National Park in Wyoming is the type locality for this parasite. Since 1893 there have been

TABLE VII. DISTRIBUTION OF THE CARYOPHYLLAEIDAE ACCORDING TO HOSTS

Parasite	Host	Locality
**Caryophyllaeus laticeps* (Pallas 1781)	*Abramis brama*	Sweden; Don R., Russia
	Cyprinus carpio	Europe
	Barbus tropidolepis	L. Tanganyika, Africa
	and 20 others noted by Lühe 1910	
**Caryophyllaeus terebrans* (Linton 1893)	*Catostomus ardens*	Heart Lake, Wyo.
	Ictiobus bubalus	Tallahatchie R., Miss.
Caryophyllaeus syrdarjensis Skrjabin 1913	*Schizothorax intermedius*	Russo-Turkestan, Asia
Caryophyllaeus armeniacus Cholodkowsky 1915	Capoëta sp.	Armenian Russia, Asia
**Caryophyllaeus caspicus* Klopina 1919	*Abramis brama*	Near Caspian Sea, Russia
	A. sopa	Near Caspian Sea, Russia
	Vimbra vimbra	Near Caspian Sea, Russia
Caryophyllaeus fimbriceps Klopina 1919	*Cyrpinus carpio*	Near Caspian Sea, Russia
Caryophyllaeus javanicus Bovien 1926	*Clarias batrachus*	Djombang, Java
Caryophyllaeus oxycephalus Bovien 1926	*Clarias batrachus*	Djombang, Java
Caryophyllaeus serialis Bovien 1926	*Clarias batrachus*	Djombang, Java
Caryophyllaeus tenuicollis Bovien 1926	*Clarias batrachus*	Djombang, Java
**Caryophyllaeus microcephalus* Bovien 1926	*Clarias batrachus*	Djombang, Java
	Macrones nigriceps	Djombang, Java
**Caryophyllaeus acutus* Bovien 1926	*Clarias batrachus*	Djombang, Java
	Macrones nigriceps	Djombang, Java
Caryophyllaeus gotoi Motomura 1927	*Misgurnus anguillicaudatus* (Cobitidae)	Kumkan R., Korea
Monobothrium wageneri (=*M. tuba* Diesing) Nybelin 1922	*Tinca chrysitis*	Italy

* Indicates species considered under "Caryophyllaeidae occurring in two or more species of fish."

DISTRIBUTION OF THE CARYOPHYLLAEIDAE ACCORDING TO HOSTS (*continued*)

Parasite	Host	Locality
Monobothrium ingens Hunter 1927	*Ictiobus cyprinella*	Mississippi R., Minn.
Glaridacris catostomi Cooper 1920	*Catostomus commersonii*	Douglas L., Mich.; Burntside L., Minn.; Lake Erie, N. Y.
Glaridacris hexacotyle (Linton 1897)	Catostomus sp.	Gila and Salt Rivers, Ariz.
Glaridacris laruei (Lamont 1921)	*Catostomus commersonii*	Green Lake and L. Mendota, Wis.; Douglas L., Mich.
**Glaridacris confusus* Hunter 1929	Ictiobus sp.	Tallahatchie R., Miss.
	Dorosoma cepedianum	Tallahatchie R., Miss.
	Ictiobus bubalus	Mississippi R., Ia.
**Caryophyllaeides fennica* (Schneider 1902)	*Leuciscus erythrophthalmus*	Finnland
	L. idus	Finnland
	L. rutilus	Sweden
Caryophyllaeides skrjabini (Popoff 1924)	*Abramis brama*	Don R., Russia
Biacetabulum infrequens Hunter 1927	*Moxostoma anisurum*	Rock R., Ill.
Biacetabulum meridianum Hunter 1929	*Erimyzon sucetta*	Eno R., No. Carolina
**Biacetabulum giganteum* Hunter 1929	Ictiobus sp.	Tallahatchie R., Miss.
	I. bubalus	Tallahatchie R., Miss.; Mississippi R., Ia.
	I. cyprinella	Rock R., Ill.; Mississippi R., Minn.
**Hypocaryophyllaeus paratarius* Hunter 1927	*Carpiodes carpio*	Rock R., Ill.
	C. velifer	Rock R., Ill.
	I. cyprinella	Mississippi R., Ia.
Archigetes sieboldi Leuckart 1878	Tubificidae	Europe
Archigetes brachyurus Mrázek 1908	Tubificidae	Europe
Archigetes cryptobothrius Wisniewski 1928	Tubificidae	Europe

Distribution of the Caryophyllaeidae According to Hosts (*Concluded*)

Parasite	Host	Locality
Lytocestus adhaerens Cohn 1908	*Clarias fuscus*	Hongkong
Lytocestus filiformis (Woodland 1923)	*Mormyrus caschive*	Anglo-Egyptian Sudan
†*Lytocestus indicus* (Moghe 1925)	*Clarias batrachus*	India
Balanotaenia bancrofti Johnston 1924	*Tandanus tandanus*	Burnett R., Queensland, Australia
Monobothroides cunningtoni Fuhrmann and Baer 1925	*Auchenoglanis occidentalis*	L. Tanganyika, Africa
Monobothroides chalmersius (?) (Woodland 1924)	*Clarias anguillaris*	Anglo Egyptian Sudan
Djombangia penetrans Bovien 1926	*Clarias batrachus*	Djombang, Java
Lytocestoides tanganyikae Baylis 1928	Alestes sp. (?)	L. Tanganyika, Africa
**Capingens singularis* Hunter 1927	*Carpiodes carpio*	Rock R., Ill.
	Ictiobus urus	Mississippi R., Minn.
Pseudolytocestus differtus Hunter 1929	*Ictiobus bubalus*	Tallahatchie R., Miss.
**Spartoides wardi* Hunter 1929	*I. cyprinella*	Rock R., Ill.; Mississippi R., Minn.
	Carpiodes thompsoni	Mississippi R., Minn.
	C. carpio	Mississippi R., Ia.
Wenyonia virilis Woodland 1923	*Synodontis schall*	Anglo-Egyptian Sudan
Wenyonia acuminata Woodland 1923	*S. membranaceus*	Anglo-Egyptian Sudan
Wenyonia minuta Woodland 1923	*Chrysichthys auratus*	Anglo-Egyptian Sudan

no other records of this form until Dr. Parke H. Simer made his collections in Mississippi in the spring of 1927. An examination of the parasites taken revealed the presence of *C. terebrans* in the intestine of *I. bubalus* taken from the Tallahatchie River. This river unites with the Yalobusha to form the Yazoo River which in turn empties into the Mississippi River above Vicksburg, Miss. The Mississippi River receives the Missouri as one of its major tributaries and this in turn is fed by the Yellowstone River which takes its origin from Yellowstone Lake in Yellowstone National Park; this lake is a relatively short distance from Heart Lake the type locality

† Woodland (1926) provisionally places this form in the genus Lytocestus. This was substantiated in a recent letter from Professor Moghe.

of this parasite. During the past glacial periods these lakes may have been connected and this would account for the appearance of this parasite in two such different watersheds, for Heart Lake is the head waters of the Snake River which flows into the Columbia River and thence to the Pacific.

The author spent several days on Heart Lake in the summer of 1925 trying to secure *Catostomus ardens*, but the attempt was unsuccessful.

Glaridacris confusus

This parasite was first found in *Ictiobus bubalus* taken from the Mississippi River near Fairport, Iowa. It was quite common in this host but was not found in *I. cyprinella* and *I. urus*, from the same locality. Dr. Parke H. Simer collected this parasite from Ictiobus sp. in the Tallahatchie River, Mississippi. The connection between this and the Mississippi River by the Yazoo River has been previously mentioned. It is probable since the waters are connected and since the other species of the genus Ictiobus did not harbor *G. confusus* that Dr. Simer's host was also *I. bubalus*.

One of the most interesting records is the finding of this parasite in *Dorosma cepedianum*. This fish is seldom parasitized and then only with Acanthocephala according to over four hundred examinations made (Van Cleave, 1916, Essex and Hunter, 1926). Furthermore this is the first record of a Cestodarian parasite in the Dorosomidae, which is in the order Isospondyli while the Catostomidae and Cyprinidae are in the Eventognathi. Since Dr. Simer examined a number of these fish and found but this one case of infection and since Essex and Hunter (1926) do not report any Cestodarian infection it appears that this was probably a case of accidental parasitism. This view is further substantiated by the existence of flood water during the time the collections were being made. Such a flood as the Mississippi River drainage experienced in 1927 would be very apt to upset the balance of fish food, and so would account for the presence of such a parasite as *G. confusus* (Hunter, 1929a).

Caryophyllaeides fennica

This parasite was reported from three different hosts from Finland and Sweden, *Leuciscus erythrophthalmus*, *L. idus*, and *L. rutilus*.

Hypocaryophyllaeus paratarius

This parasite was very common in the fish taken from the Rock and Mississippi rivers. Both *Carpiodes carpio* and *C. velifer* harbored *H. paratarius* when taken from the Rock River although similar hosts examined from the latter river near Fairport, Iowa did not yield this form; however the parasite was found in *Ictiobus cyprinella*. Since the feeding habits and the food of Carpiodes and Ictiobus are rather similar one might suppose that the host was largely a matter of chance among these and related forms.

Capingens singularis

Capingens singularis was found but twice in an examination of over 600 fish. It was recovered once from the stomach of *Carpiodes carpio* and once from *Ictiobus urus*. The former was taken from the Rock River and the latter from Lake Pepin, an expansion of the Mississippi River, between Minnesota and Wisconsin. Each infection occurred singly, and these were the only two records of this form ever found.

Spartoides wardi

Spartiodes wardi was commonly found in *Ictiobus cyprinella* taken from both the Rock and Mississippi Rivers. The former empties into the Mississippi near Moline, Illinois which is less than twenty miles above the spot where the species was taken from the latter locality. Likewise *Carpiodes carpio* taken from the aforementioned localities yielded the same parasites. Another species of the same genus, *C. thompsoni*, which is limited in distribution to Lake Pepin in the Mississippi drainage was also found to shelter *S. wardi*. These four hosts and the three different localities indicate a very wide distribution for this parasite.

Biacetabulum giganteum

This species was reported from two hosts from the Tallahatchie River in Mississippi, Ictiobus sp. and *I. bubalus*. This latter host also harbored the same parasite when taken from the Mississippi River at Fairport, Iowa. There is nothing unusual about this since the host is found in numbers in both localities and is one of the most common buffalo fish. Still another host, *I. cyprinella*, when examined from the Rock River in Illinois and Lake Pepin in the upper Mississippi River between Wisconsin and Minnesota yielded *B. giganteum*. This host is likewise common in both of these regions. The records show wide distribution for this form.

Caryophyllaeus microcephalus

This parasite was recovered from two species of catfish, *Clarias batrachus* and *Macrones nigriceps*, from streams near Djombang, Java. From the records it appears that both hosts occurred in the same stream and the same general locality. The former acted as a host for five other species in Java and one from Asia. It is a well established geological fact that the entire archipelago off the tip of the Malay Penninsula was connected during the past geologic ages. This may help account for the distribution of these parasites on the comparatively isolated islands of that group. Incidentally it opens up some very interesting problems through a study of the hosts and their parasites in an attempt to determine which islands were connected to the mainland and which were always separated.

Caryophyllaeus acutus

This parasite was likewise recovered from *Clarias batrachus* and *Macrones nigriceps* which were taken in the vicinity of Djombang, Java.

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EXPLANATION OF PLATES

Abbreviations

a	acetabular sucker	*olm*	outer longitudinal muscle
b	bothrium	*om*	ovarian commissure
bm	basement membrane	*ot*	oötype
c	circular muscles of cuticula	*p*	post-ovarian vitelline duct
cs	cirrus sac	*r*	receptaculum seminis
d	ductus ejaculatorius	*s*	seminal vesicle
e	excretory canals	*sh*	gland cell of oötype
ea	ascending excretory canal	*sp*	sphincter muscle
ed	descending excretory canal	*t*	testis
eb	excretory bladder	*td*	terminal disc
f	fertilization chamber	*tr*	transverse muscle
g	ganglionic mass	*u*	uterus
ga	genital atrium	u^1	primary descending limb of uterus
gm	gland cell of parenchyma	u^2	ascending limb of uterus
i	inner longitudinal muscle	u^3	descending limb of uterus
it	terminal introvert	*uv*	utero-vaginal canal
l	loculus	*v*	vagina
lc	longitudinal cuticular muscle	*vd*	vas deferens
o	ovary	*vtd*	vitelline duct
ob	oblique muscle	*x*	successive stages
oc	oöcapt	*y*	in formation of
od	oviduct	*z*	vitelline follicles

The lines in the figures have the following values: 0.02 mm. in figures 69, 77, 78, 81; 0.05 mm. in figures 76, 80, 84; 0.2 mm. in figures 5, 6, 27, 49, 54–60, 62–65, 68, 70, 85–90; and 0.5 mm. in all other figures.

PLATE I

EXPLANATION OF PLATE I

FIG. 1. *Caryophyllaeus terebrans*, scolex.
FIG. 2. *Glaridacris catostomi*, scolex.
FIG. 3. *G. hexacotyle*, scolex.
FIG. 4. *G. laruei*, scolex.
FIG. 5. *Hypocaryophyllaeus paratarius*, scolex.
FIG. 6. *H. paratarius*, sagittal section showing inner longitudinal muscles.
FIG. 7. *H. paratarius*, larva.
FIG. 8. *Monobothrium ingens*, scolex.
FIG. 9. *M. ingens*, cross section through terminal introvert.
FIG. 10. *Capingens singularis*, scolex.
FIG 11. *C. singularis*, cross section through bothria.
FIG. 12. *Biacetabulum infrequens*, scolex.

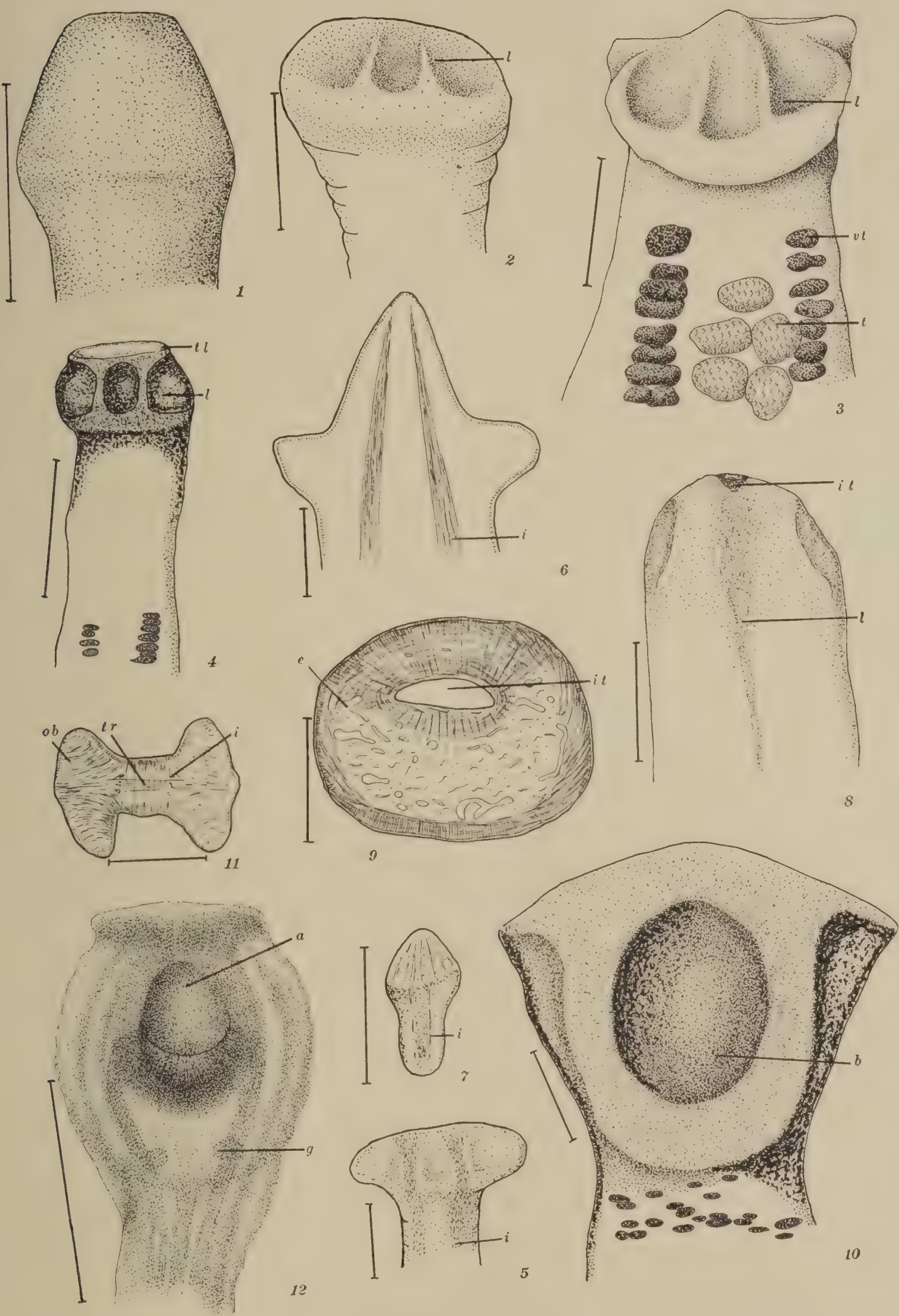
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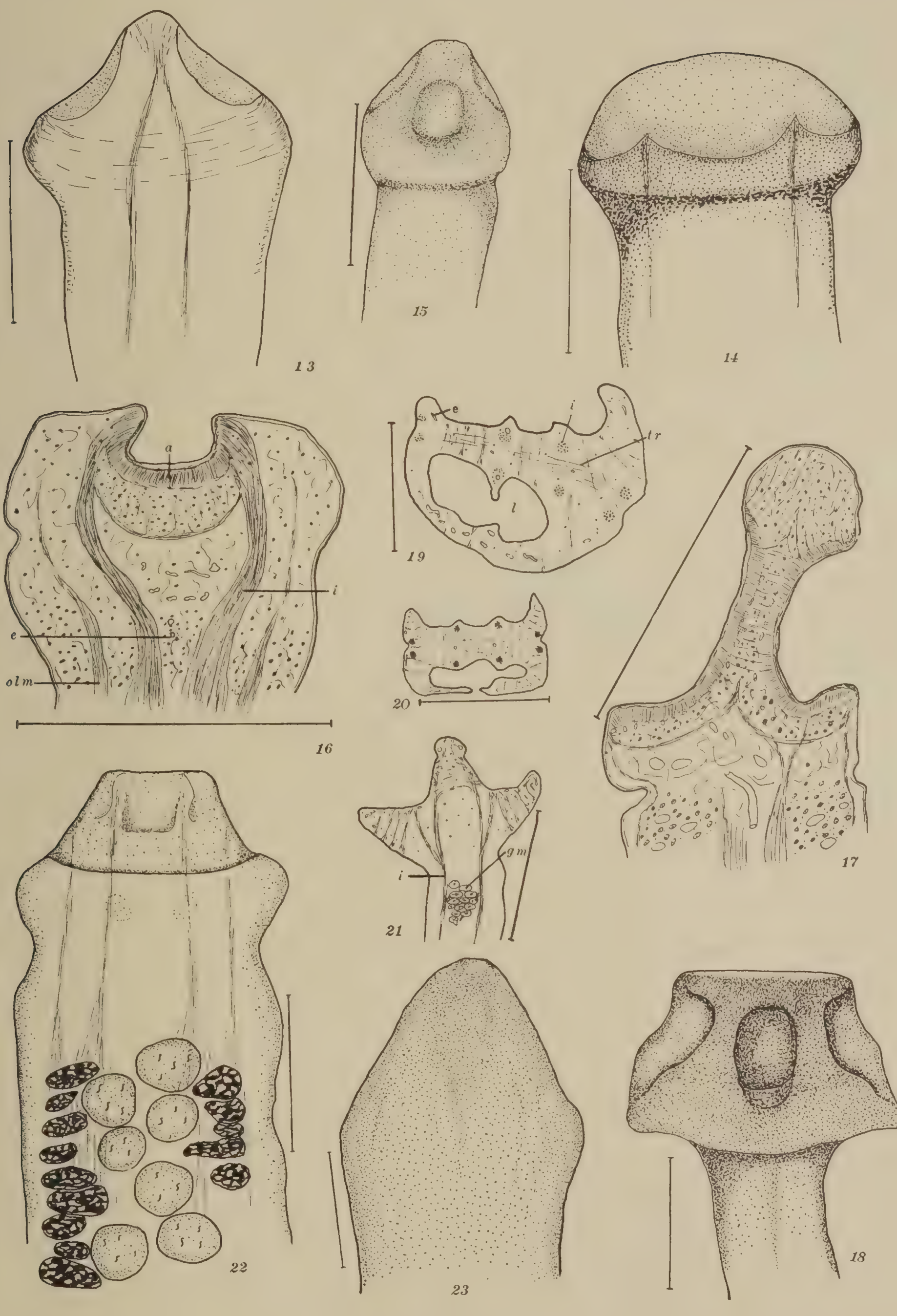
PLATE II

EXPLANATION OF PLATE II

FIG. 13. *Spartoides wardi*, lateral view of scolex.
FIG. 14. *S. wardi*, scolex.
FIG. 15. *Biacetabulum meridianum*, scolex.
FIG. 16. *B. infrequens*, frontal section, through acetabular sucker.
FIG. 17. *B. infrequens*, sagittal section, through scolex.
FIG. 18. *B. giganteum*, scolex.
FIG. 19. *Glaridacris hexacotyle*, cross section, through scolex.
FIG. 20. *G. hexacotyle*, cross section, through scolex.
FIG. 21. *G. hexacotyle*, sagittal section, through scolex.
FIG. 22. *G. confusus*, scolex.
FIG. 23. *Pseudolytocestus differtus*, scolex.



HUNTER CARYOPHYLLAEIDAE PLATE II

PLATE III

EXPLANATION OF PLATE III

Fig. 24. *Glaridacris confusus*, toto, reproductive systems.
Fig. 25. *G. catostomi*, toto, reproductive systems.
Fig. 26. *Pseudolytocestus differtus*, toto, reproductive systems.
Fig. 27. *Hypocaryophyllaeus paratarius*, cross section, through scolex.
Fig. 28. *Spartoides wardi*, toto, reproductive systems.
Fig. 29. *Monobothium ingens*, toto, reproductive systems.
Fig. 30. *Caryophyllaeus terebrans*, toto, reproductive systems.
Fig. 31. *C. terebrans*, frontal section, reproductive systems.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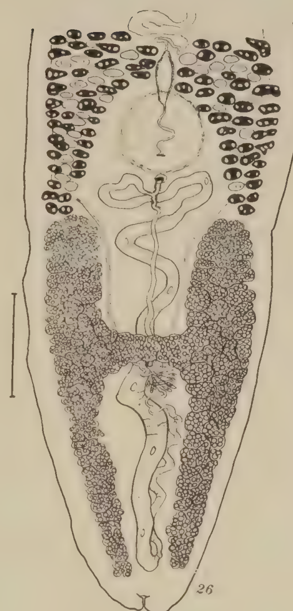
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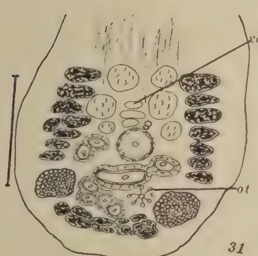

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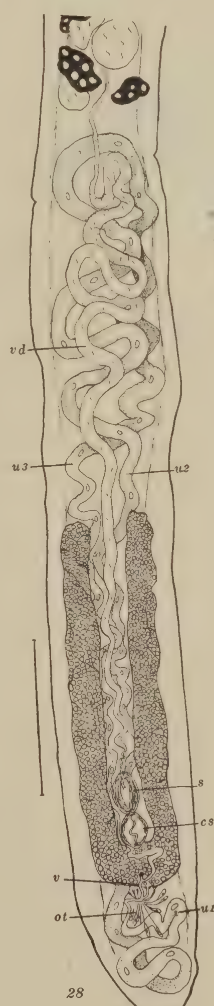

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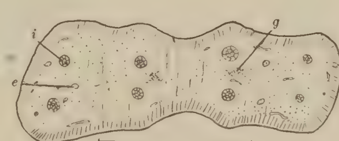

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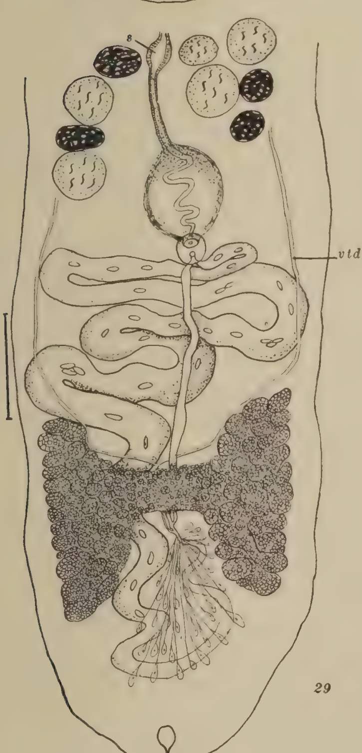

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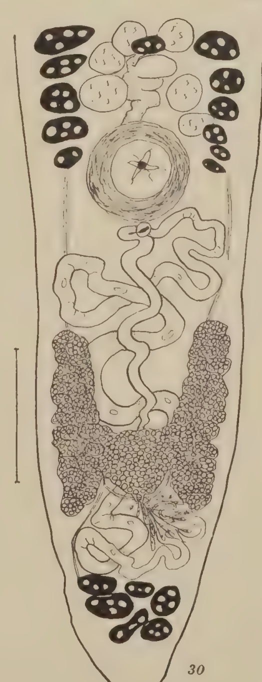
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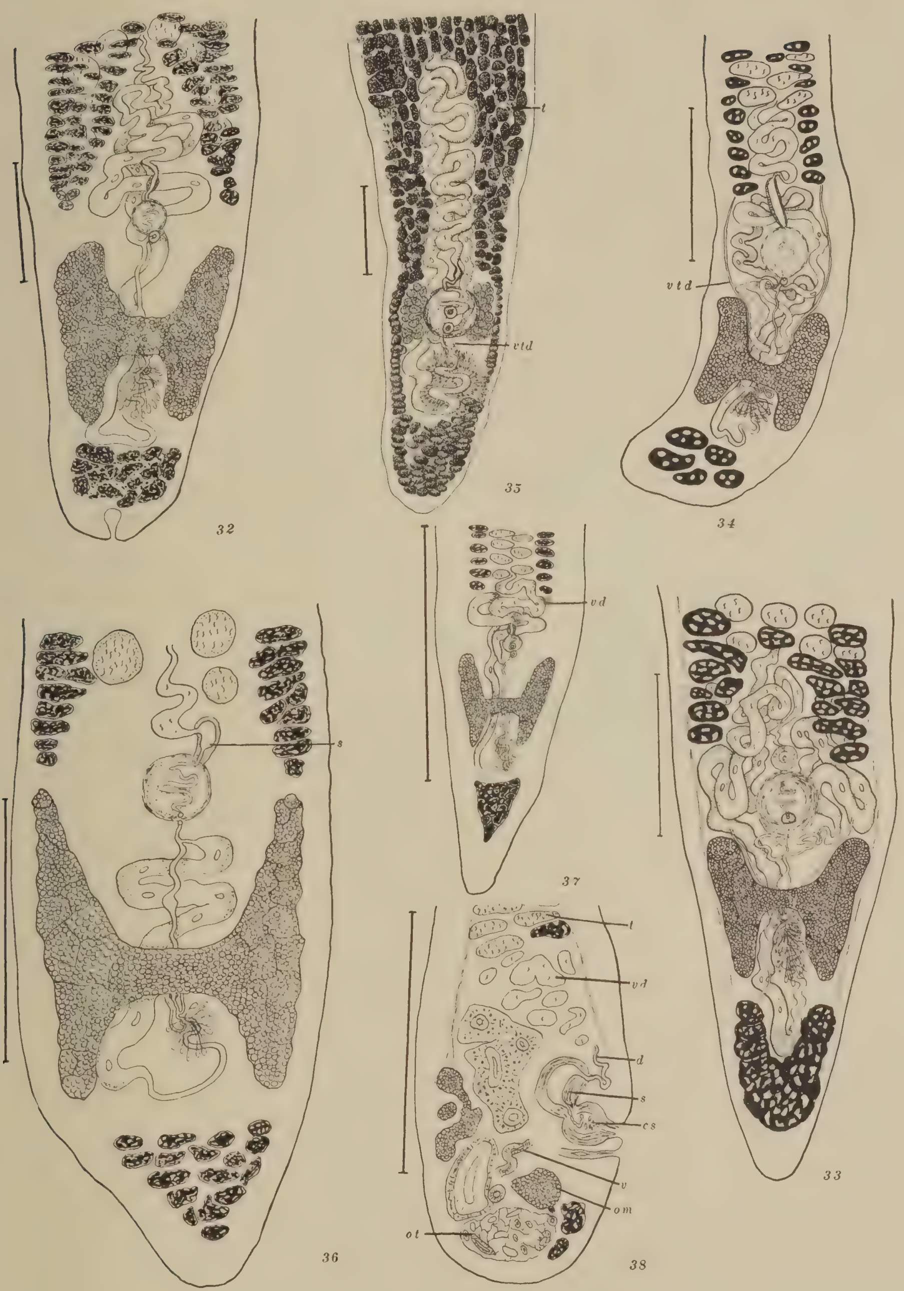
PLATE IV

EXPLANATION OF PLATE IV

Fig. 32. *Biacetabulum infrequens*, toto, reproductive systems.
Fig. 33. *B. giganteum*, toto, reproductive systems.
Fig. 34. *B. meridianum*, toto, reproductive systems.
Fig. 35. *Capingens singularis*, toto, reproductive systems.
Fig. 36. *Glaridacris laruei*, toto, reproductive systems.
Fig. 37. *Hypocaryophyllaeus paratarius*, toto, reproductive systems.
Fig. 38. *H. paratarius*, sagittal section, through reproductive systems.



HUNTER CARYOPHYLLAEIDAE PLATE IV

PLATE V

EXPLANATION OF PLATE V

FIG. 39. *Monobothrium ingens*, sagittal section, through reproductive systems.
FIG. 40. *Biacetabulum giganteum*, sagittal section, through reproductive systems.
FIG. 41. *Glaridacris hexacotyle*, sagittal section, through reproductive systems.
FIG. 42. *G. hexacotyle*, cross section, through testes.
FIG. 43. *G. confusus*, sagittal section, through reproductive systems.
FIG. 44. *G. catostomi*, sagittal sections, through reproductive systems.
FIG. 45. *G. catostomi*, cross section, through testes.
FIG. 46. *Biacetabulum meridianum*, sagittal section, through reproductive systems.
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FIG. 51. *Caryophyllaeus terebrans*, frontal section, through reproductive systems.
FIG. 52. *Pseudolytocestus differtus*, sagittal section, through reproductive systems.

HUNTER CARYOPHYLLAEIDAE PLATE V

PLATE VI

EXPLANATION OF PLATE VI

FIG. 53. *Biacetabulum giganteum*, cross section, through testes.
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FIG. 55. *B. giganteum*, cross section, through scolex 100μ from tip.
FIG. 56. *B. giganteum*, cross section, through scolex 200μ from tip.
FIG. 57. *B. giganteum*, cross section, through scolex 290μ from tip.
FIG. 58. *B. giganteum*, cross section, through scolex 490μ from tip.
FIG. 59. *B. giganteum*, cross section, through scolex 700μ from tip.
FIG. 60. *B. giganteum*, cross section, through scolex 1 mm. from tip.
FIG. 61. *Spartoides wardi*, cross section, through scolex.
FIG. 62. *S. wardi*, cross section, through base of scolex.
FIG. 63. *S. wardi*, cross section, through testes.
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FIG. 65. *B. meridianum*, cross section, through acetabular-like sucker.
FIG. 66. *Glaridacris confusus*, outline of cross sections through scolex; figures indicate micra from distal extremity.
FIG. 67. *G. confusus*, cross section, through base of scolex.
FIG. 68. *G. confusus*, cross section, through testes
FIG. 69. *Biacetabulum infrequens*, cell from wall of seminal vesicle.
FIG. 70. *B. infrequens*, cross section, through testes.
FIG. 71. *Pseudolytocestus differtus*, cross section, through base of scolex.
FIG. 72. *Caryophyllaeus terebrans*, cross section, through testes.

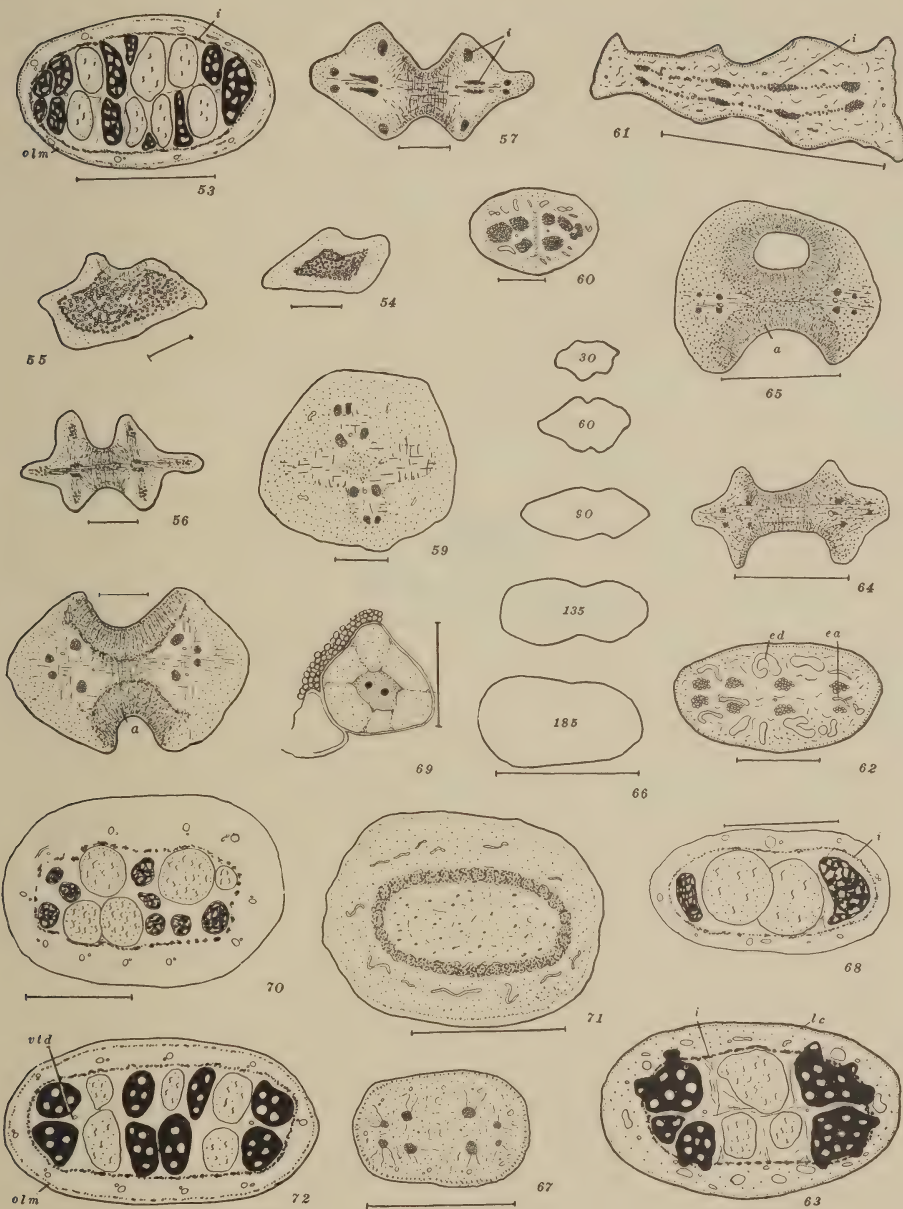
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PLATE VII

EXPLANATION OF PLATE VII

Fig. 73. *Capingens singularis*, cross section through testes.
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Fig. 75. *C. singularis*, cross section, through utero-vaginal canal.
Fig. 76. *C. singularis*, cross section, through oötype.
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Fig. 78. *Glaridacris laruei*, egg.
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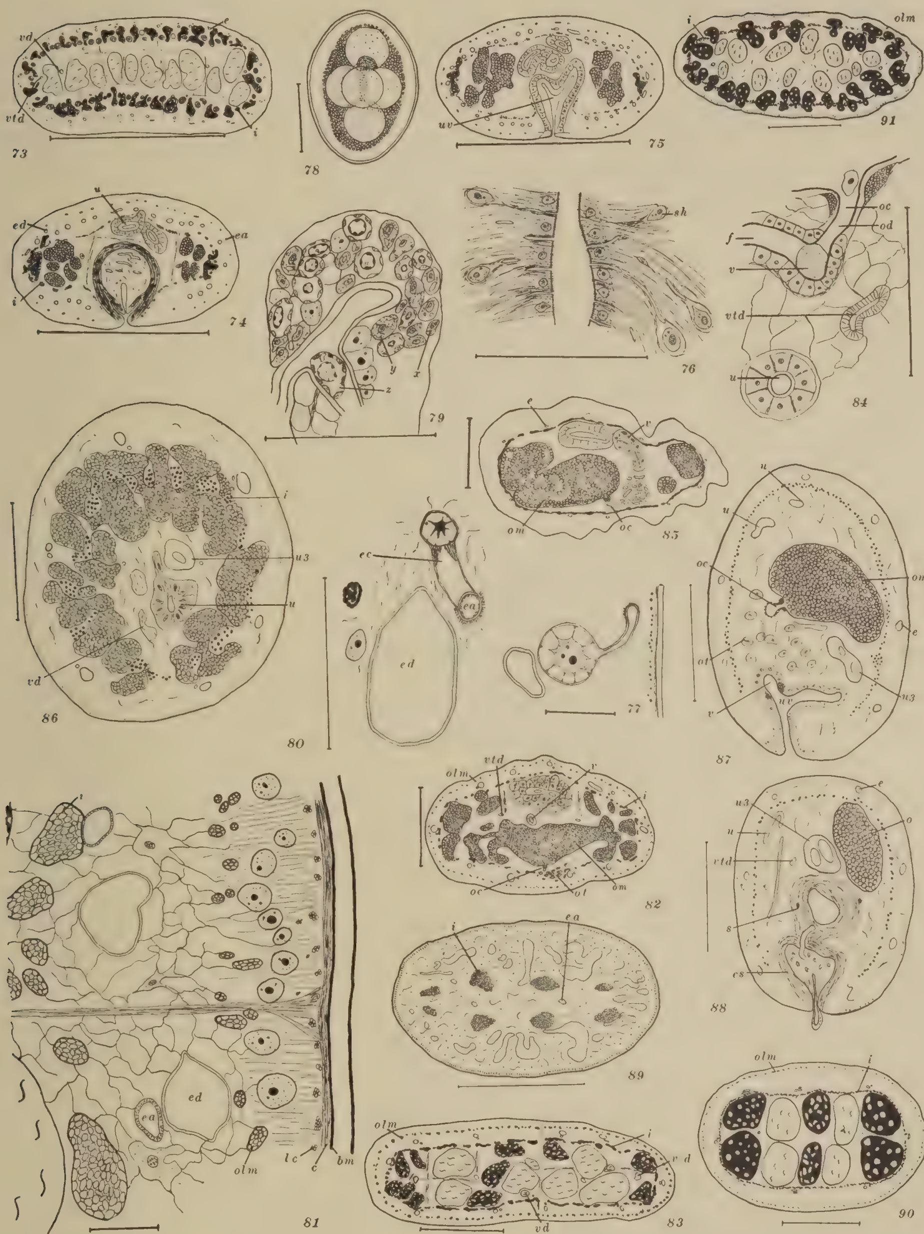
Fig. 90. *Biacetabulum meridianum*, cross section, through testes.
Fig. 91. *Pseudolytocestus differtus*, cross section, through testes.



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Vol. XI October, 1927 No. 4

STUDIES ON THE CARYOPHYLLAEIDAE OF NORTH AMERICA

WITH SEVEN PLATES

BY

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